

<https://helda.helsinki.fi>

---

## Interannual variation and long-term trends in proportions of resident individuals in partially migratory birds

Meller, Kalle

2016-03

---

Meller , K , Vahatalo , A V , Hokkanen , T , Rintala , J , Piha , M & Lehikoinen , A 2016 , ' Interannual variation and long-term trends in proportions of resident individuals in partially migratory birds ' , Journal of Animal Ecology , vol. 85 , no. 2 , pp. 570-580 . <https://doi.org/10.1111/1365-2656.12486>

---

<http://hdl.handle.net/10138/231228>

<https://doi.org/10.1111/1365-2656.12486>

---

---

*Downloaded from Helda, University of Helsinki institutional repository.*

*This is an electronic reprint of the original article.*

*This reprint may differ from the original in pagination and typographic detail.*

*Please cite the original version.*

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/288838523>

# Inter-annual variation and long-term trends in proportions of resident individuals in partially migratory birds

Article in *Journal of Animal Ecology* · December 2015

DOI: 10.1111/1365-2656.12486

CITATIONS

6

READS

121

6 authors, including:



**Anssi Vähätalo**

University of Jyväskylä

73 PUBLICATIONS 1,835 CITATIONS

[SEE PROFILE](#)



**Jukka Rintala**

Natural Resources Institute Finland (Luke)

35 PUBLICATIONS 378 CITATIONS

[SEE PROFILE](#)



**Markus Piha**

University of Helsinki

37 PUBLICATIONS 352 CITATIONS

[SEE PROFILE](#)



**Aleksi Lehikoinen**

University of Helsinki

103 PUBLICATIONS 1,776 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Population dynamics of passerines - Constant Effort Sites scheme [View project](#)



Long term changes in biometrics of birds [View project](#)

1 **Inter-annual variation and long-term trends in proportions of resident individuals in partially migratory**  
2 **birds**

3

4 Kalle Meller<sup>\*a</sup>, Anssi V. Vähätalo<sup>b</sup>, Tatu Hokkanen<sup>c</sup>, Jukka Rintala<sup>d</sup>, Markus Piha<sup>a</sup> and  
5 Aleksi Lehikoinen<sup>a</sup>

6

7 <sup>a</sup>The Helsinki Lab of Ornithology, The Finnish Museum of Natural History, University of Helsinki, Helsinki,  
8 Finland

9 <sup>b</sup>Department of Biological and Environmental Science, University of Jyväskylä, Jyväskylä, Finland

10 <sup>c</sup> Natural Resources Institute Finland, P.O. Box 18, FI-01301, Vantaa, Finland

11 <sup>d</sup> Natural Resources Institute Finland, P.O. Box 2, FI-00791, Helsinki, Finland

12 <sup>\*</sup> Corresponding author: kalle.meller@helsinki.fi

13 **Summary**

14 1. Partial migration – a part of a population migrates and another part stays resident year-round on the breeding  
15 site – is probably the most common type of migration in the animal kingdom, yet it has only lately garnered  
16 more attention. Theoretical studies indicate that in partially migratory populations the proportion of resident  
17 individuals (PoR) should increase in high latitudes in response to the warming climate, but empirical evidence  
18 exists for few species.

19

20 2. We provide the first comprehensive overview of the environmental factors affecting PoR and the long-term  
21 trends in PoR by studying 27 common partially migratory bird species in Finland.

22

23 3. The annual PoR values were calculated by dividing the winter bird abundances by the preceding breeding  
24 abundances. First, we analysed whether early-winter temperature, winter temperature year before or the

25 abundance of tree seeds just before overwintering, explain the inter-annual variation in PoR. Second, we  
26 analysed the trends in PoR between 1987 and 2011.

27

28 4. Early-winter temperature explained the inter-annual variation in PoR in the waterbirds (waterfowl and gulls),  
29 most likely because the temperature affects the ice conditions and thereby the feeding opportunities for the  
30 waterbirds. In terrestrial species, the abundance of seeds was the best explanatory variable. Previous winter's  
31 temperature did not explain PoR in any species, thus we conclude that variation in food availability caused the  
32 inter-annual variation in PoR. During the study period PoR increased in waterbirds but did not change in  
33 terrestrial birds.

34

35 5. Partially migratory species living in physically contrasting habitats can differ in their annual and long-term  
36 population-level behavioural responses to warming climate, possibly because warm winter temperatures reduce  
37 ice cover and improve the feeding possibilities of waterbirds but do not directly regulate the food availability for  
38 terrestrial birds.

39

40 **Key-words** animal movement, bird feeding, climate change, density-dependent strategy, fluctuating food  
41 availability, non-breeding habitat quality, range shift, wintering area

42

## 43 **Introduction**

44 Many species migrate annually between breeding and wintering areas in response to seasonal fluctuation in  
45 temperature and food availability (Alerstam 1990). Partial migration is a strategy where a part of a population  
46 migrates away from the breeding area (hereafter migrants), whereas the other part lives on the same area year-  
47 round (hereafter residents, Terrill & Able 1988). Partial migration emerges in a population when the individuals

48 confront contradictory selection pressures concerning migration: a part of a population achieves higher fitness by  
49 migrating whereas the other part achieves higher fitness by being resident (Kaitala, Kaitala & Lundberg 1993).  
50 The fitness consequences of overwintering in a certain place must be regulated by density dependence for partial  
51 migration to emerge because otherwise it would simply be most beneficial for all individuals to overwinter in the  
52 same area, *i.e.* either to migrate or to stay resident (Taylor & Norris 2007). Genetic studies indicate that the  
53 potential for changes in migration patterns is well preserved in populations (Pulido 2011) and a rapid change  
54 from a migratory to sedentary population can occur when selection pressures change (Berthold, Mohr & Querner  
55 1990).

56         The inter-annual variation in food availability affects the migration behaviour of some partially  
57 migratory species (Fox *et al.* 2009; Lindén *et al.* 2011). In the boreal zone, the seeds of several tree species are  
58 important but fluctuating food resource for wintering animals. The inter-annual variation in seed crops causes  
59 variation in the wintering numbers of many seed- and berry-eating (hereafter frugivorous) birds (Haila, Tiainen  
60 & Vepsäläinen 1986).

61         One of the most important environmental variables affecting migration strategies is temperature, as  
62 demonstrated by the increase of the proportion of migratory bird species towards the poles (Newton & Dale  
63 1996). In high latitudes or altitudes, wintering on or near the breeding site is risky because cold winters increase  
64 the energy expenditure of individuals and even can cause mortality (Robinson, Baillie & Crick 2007). On the  
65 other hand, wintering in the breeding area has many beneficial effects, like avoiding risky migration (Sillett &  
66 Holmes 2002), being able to optimize breeding phenology according to progression of spring (Love *et al.* 2010)  
67 and being among the first ones to occupy a breeding territory (Kokko 2011).

68         Climate change has elevated global temperatures over the last 40 years with the most pronounced  
69 warming at higher northern latitudes during winters (IPCC 2013). An increase in winter temperature has the  
70 largest impact on the environmental conditions in regions where the mean winter temperature is near the zero °C  
71 isotherm, as in Finland. In these regions, even a small change in the temperature affects the occurrence and  
72 amount of ice and snow (Luomaranta *et al.* 2014), which influence the feeding opportunities of both terrestrial  
73 and aquatic species.

Climate warming has already shifted the breeding and wintering ranges of migratory and resident animals towards poles (*e.g.* Parmesan 2006; Brommer, Lehikoinen & Valkama 2012). The migration distances have become shorter in some species indicating a possible gradual change towards residency (Visser *et al.* 2009). In partially migratory populations, the proportion of individuals staying resident is expected to rise as the increasing winter temperatures improve food availability and survival of resident individuals (Berthold 2001, Griswold, Taylor & Norris 2011).

To our knowledge, few studies have focused on changes in proportions of residents in partially migratory species and whether the climate warming has contributed to these changes. The warming climate has increased the proportion of residents (hereafter PoR) in common blackbirds *Turdus merula* in the Netherlands (Vliet, Musters & Keurs 2009), but not in blue tits *Cyanistes caeruleus* in Sweden (Nilsson *et al.* 2006). PoR has increased also among great crested grebes *Podiceps cristatus* in the Netherlands (Adriaensen, Ulenaers & Dhondt 1993) and elks *Cervus elaphus canadensis* in North America (Hebblewhite & Merrill 2011). However, these responses were not clearly related to temperature change but were primarily explained by an increase in the amount of manmade lakes suitable for wintering and a higher predation mortality of migratory individuals, respectively. Thus, the predicted changes in PoR caused by increased winter temperatures are still poorly supported by observations.

In this study, we examined two related questions regarding PoR in 27 partially migratory bird species. First, we examined if two extrinsic environmental variables — temperature or seed crop — explained the inter-annual variation in PoR. We investigated the not mutually exclusive effects of two different kinds of temperature variables: the temperature at the beginning of the overwintering season (hereafter early-winter temperature) and the temperature of the previous winter. If PoR would be affected by early-winter temperature, it would support the idea of direct temperature effect on birds when they are deciding on whether to migrate or not (Lehikoinen *et al.* 2013). The effect of previous winter's temperature would imply either a natural selection by better (or worse) fitness of the resident part of the population compared with the migrating part, or a learned behavioural response by individuals that had successfully stayed resident during the previous winter. We quantified the seed crop of three tree species which provide the most exploited food source for overwintering frugivorous birds in Finland. We expected a positive relationship between seed abundance and annual PoR in several species. Our analyses

101 also accounted for the breeding success, as PoR may increase after a good breeding success if large number of  
102 first-winter birds overwinter close to breeding grounds.

103         Second, we analysed if PoR and the explanatory extrinsic environmental variables (seed crop and  
104 temperature) changed during the 25-year study period and examined if they had similar trends. In addition to  
105 analysing each species separately, we also divided them into two functional groups: terrestrial birds and  
106 waterbirds.

107

## 108 **Material & Methods**

### 109 *Study species, period and area*

110 We selected 27 common partially migratory species of which we had substantial long-term monitoring data of  
111 both breeding and winter monitoring schemes in Finland into our analyses (Table S1). We divided the study  
112 species into terrestrial birds and waterbirds. All 18 terrestrial species were passerines (*Passeriformes*) while  
113 waterbirds comprised two groups: six waterfowl (*Anatidae*) and three gulls (*Laridae*). The study period covers  
114 breeding seasons 1986–2010 and winters 1986/1987–2010/2011. Breeding individuals of many study species  
115 ringed in the study area have been commonly recovered wintering in Finland (Saurola et al. 2013, Valkama *et al.*  
116 2014).

117         The northern location of our study area (Finland) is suitable for investigating the changes in the  
118 proportions between residents and migrants because the northern edge of the distribution of more than two thirds  
119 of our study species is within the study area (Brommer, Lehikoinen & Valkama 2012). Because of the northern  
120 location the effect of individuals breeding and migrating from outside the study area on the results is smaller  
121 than in more southern areas, but still an unknown proportion of wintering individuals probably arrives annually  
122 from the directions between north and east.

123

### 124 *Bird population monitoring schemes*

125 The wintering abundance of all species was based on Finnish winter bird monitoring scheme, which is  
126 coordinated by the Finnish Museum of Natural History. Annually 500 routes located across Finland and with a  
127 mean length of 10 kilometres were surveyed by foot or ski once between 25<sup>th</sup> December and 7<sup>th</sup> January  
128 (Koskimies & Väisänen 1991; Fig. 1a). Most of the routes were monitored every year, usually by the same  
129 person or people. Birds observed along the routes were identified to species level, counted and reported as the  
130 number of individuals per km for the year of January (*e.g.* winter 1989/1990 was reported as 1990).

131 The breeding population sizes of terrestrial birds were estimated by line transect counts and point counts,  
132 organized by the Finnish Museum of Natural History. About 150 line transects ca. 6 km in length and ca. 50  
133 point count routes were monitored annually mainly in June (Lehikoinen 2013; Fig. 1b). Breeding population  
134 sizes of waterbirds were estimated on the basis of inland waterbird (Pöysä *et al.* 2013) and archipelago birds  
135 censuses (Hario & Rintala 2011) organized by the Natural Resources Institute Finland and the Finnish Museum  
136 of Natural History. Waterbird censuses were conducted on the lakes and inner bays of the Baltic Sea, whereas  
137 archipelago censuses were done on the islands along the Finnish coastline of the Baltic Sea (Koskimies &  
138 Väisänen 1991, Fig. 1b). In all breeding bird censuses, individual birds, pairs, nests and local flocks were  
139 interpreted into units of pairs, whereas in winter bird censuses the unit was the individual (Table S1).

140 The spatial coverage of the breeding counts is better in the northern part of the country compared to the  
141 wintering counts. However, we do not believe that this is a major problem for two reasons. First, both breeding  
142 and wintering abundances of most study species are much lower in the northern part than in the southern part of  
143 Finland (Väisänen *et al.* 1998, Väisänen 2003). Second, Lehikoinen (2013) and Fraixedas *et al.* (2015) have  
144 earlier shown that there are no temporal trends in the mean latitude of the line transect and winter bird data, and  
145 thus the spatial distribution of the censuses has not changed and the ratio between counts should be comparable.  
146 We applied similar analyses to breeding waterbird census sites and constant effort sites (see later *breeding*  
147 *success index*).

148

149 *Breeding success index*

150 Wintering individuals consisted partially of adult birds surveyed during breeding time but also of juvenile



151 individuals hatched after the summer censuses. To account for the potential bias in our analyses due to inter-  
152 annual variation in the proportion of juveniles, we included the *breeding success index (BS)* in our analysis as  
153 proxy of the effect of juvenile individuals on winter numbers. The breeding success of passerines was estimated  
154 using data from Finnish constant effort site scheme (CES), organized by the Finnish Museum of Natural History  
155 (1987 onwards, Piha & Haapala 2012).

156         The protocol closely follows the British CES-scheme (Baillie *et al.* 1986). CES consisted of up to 12  
157 standardized mist-net catches (visits) between May and August from 151 sites. On average, 33 sites were  
158 surveyed annually. CES data covered 11 passerine species of 27 study species (Table S1). The breeding success  
159 index was calculated from the CES data as the annual probabilities of an individual being juvenile using the  
160 binomial model by Robinson *et al.* (2007).

161

#### 162 *Crop monitoring schemes and weather data*

163 The annual abundance of rowanberries *Sorbus aucuparia* was estimated during the winter bird monitoring  
164 scheme using a six-level scale: 1) none, 2) very few, 3) few, 4) moderate, 5) abundant, 6) very abundant  
165 (Koskimies & Väisänen 1991). Annual abundances of Norway spruce *Picea abies* seeds and birch (*Betula*  
166 *pendula* and *B. pubescens* combined) male catkins were calculated in seed crop monitoring stands run by the  
167 Natural Resources Institute Finland (Hokkanen 2000). The material contains on average 55 spruce stands and 56  
168 birch stands around Finland annually (Hokkanen 2000). In the schemes, the number of spruce cones and male  
169 catkins of birches, both of which are highly correlated with the amount of seeds, were used as proxies of the  
170 annual seed crop.

171         We expected that the abundance of seeds or rowanberries would influence in particular those species  
172 which use them as a food resource. Spruce seeds are the preferred food for common crossbill *Loxia curvirostra*,  
173 rowanberries for common blackbird, fieldfare *Turdus pilaris*, Eurasian bullfinch *Pyrrhula pyrrhula* and  
174 brambling *Fringilla montifringilla* and a combination of birch and spruce seeds for Eurasian siskin *Carduelis*  
175 *spinus* and common redpoll *Carduelis flammea* (Reinikainen 1937, Fox *et al.* 2009, Lehikoinen, Väisänen &  
176 Hokkanen 2010). Food availability does not only affect the number of wintering birds, but also the timing of

177 autumn migration which occurs earlier during a low crop situation (Fox et al. 2009). The annual abundance of  
178 seeds or rowanberries was defined as crop ( $C$ ), which for rowanberry was calculated as the mean abundance  
179 observed at the monitoring sites. For birch and spruce,  $C$  was calculated as the  $\log_{10}$ -transformed mean of the  
180 annual abundance of catkins or cones observed at the monitoring sites. For non-specialist birds,  $C$  was defined as  
181 the mean of the annual crop of three tree species after they had been scaled to have an average of 0 and a  
182 standard deviation of 1. This describes the general crop situation, because the annual seed and rowanberry crops  
183 were correlated (Pearson correlations between 0.46 and 0.65; Fig. 2a).

184         Daily mean temperature data covering Finland with a 10 km grid resolution was obtained from the  
185 Finnish Meteorological Institute (Venäläinen *et al.* 2005). We calculated the early- and midwinter temperatures  
186 for each species from November to December and from December to February, respectively (Fig. 2b). For the  
187 species-specific calculations, we used only those grid cells where a species had been observed at least once in  
188 the winter censuses during the whole study period. The midwinter temperature of the previous year was used to  
189 account for the evolutionary selection response or learned behaviour to be more (or less) inclined to stay resident  
190 due to the temperature-induced success of the previous wintering attempt of resident individuals.

191

#### 192 *Annual indices of summer and winter bird abundances*

193 The annual abundances of each species from breeding censuses and winter bird counts were modelled into  
194 species-specific annual summer and winter abundance indices using TRIM-software (version 3.54, Pannekoek &  
195 Van Strien 2005), which was developed for the analysis of time series of counts obtained from monitoring  
196 wildlife populations and is commonly used in the European bird monitoring schemes (*e.g.* Gregory *et al.* 2005).  
197 TRIM-software applies generalized estimation equations approach for estimating loglinear models. We used  
198 TRIM to impute the missing counts of repeatedly surveyed routes or points into our time-series using the option  
199 of 'time effects models with overdispersion and serial correlation'. The imputed annual indices were used as the  
200 annual summer and winter abundance indices in the latter analyses. Because the method did not allow years to  
201 have zero observed individuals, for the common starling *Sturnus vulgaris* with winter 2010/2011 with zero  
202 observations we added, before inputting data to TRIM, one individual for the winter census route where the

203 species had been observed the most times.

204 In order to examine the relative importance summer and winter indices had on PoR, we compared the  
205 species-specific coefficients of variation (CV). In addition, we compared the precisions of summer and winter  
206 indices by analysing the differences in the species-specific means of the annual relative standard errors (RSE, the  
207 standard error divided by the mean and multiplied by 100). The testing was done using paired t-tests.

208

#### 209 *Proportion of residents (PoR)*

210 We defined the individuals observed inside Finnish borders during the winter counts as residents, while migrants  
211 were the individuals which had migrated away from Finland and therefore were not observed in the winter  
212 counts. Our division of individuals into residents and migrants was dictated by the monitoring area (Finland) and  
213 therefore was partly an arbitrary one, as it inevitably always is unless the individual choice of leaving or staying  
214 inside a breeding territory is monitored. However, the Baltic Sea delineates the main migration direction (south-  
215 southwest) and thereby forms a natural barrier for migration, particularly for the terrestrial species.

216 The annual summer and winter abundance indices from TRIM were used to calculate the annual PoR for  
217 each species by dividing the annual winter abundance index by the annual summer abundance index of the  
218 preceding summer. Hence, PoR is not a proportion ranging from zero to one, but a proportion relative to the  
219 situation in the first year of the study period (1987) *i.e.* base year, whose indices were set to one. Neither does  
220 PoR represent the real proportion of residents in the total population. Although the actual proportions of  
221 residents were not known, the real proportion of residents in the total population are known to vary a lot among  
222 our study species (Koskimies 1993). For example, a large proportion of yellowhammers *Emberiza citrinella* and  
223 tits overwinter in Finland, but starlings and reed buntings *Emberiza schoeniclus* primarily spend their winters  
224 away from Finland. In order to achieve linearity, *PoR* was  $\log_{10}$ -transformed.

225

#### 226 *Analyses of the inter-annual variation in PoR*

227 We applied an information-theoretic approach based on AICc values (Akaike's information criterion for a small  
228 sample size, Burnham & Anderson 2002) in order to estimate the importance of explanatory variables (seed  
229 crops, breeding success, early-winter temperature and previous midwinter temperature) in explaining the inter-  
230 annual variation in PoR. For every species, we constructed a set of eight or sixteen (depending on whether  
231 breeding success data was available) competing general linear models with all main-effect combinations of three  
232 or four explanatory variables (Table S2). In order to identify general patterns for waterbirds and terrestrial birds  
233 as distinct functional groups, we constructed two random-intercept mixed models with the same set of covariates  
234 but excluding breeding success data and using species as a random factor with package *nlme* in R (Pinheiro *et al.*  
235 2014). Further, because the feeding opportunities of frugivorous species are strongly affected by tree seed and  
236 berry crops which usually vary biannually (Fox *et al.* 2009; Lindén *et al.* 2011, Fig. 2a), we expected PoR of  
237 frugivores to be less directly influenced by temperature. Therefore, to exclude a potential bias when including  
238 these food-specialists in our comparison of the species of aquatic and terrestrial habitats, we formed a third  
239 functional group of terrestrial species whose inter-annual variation in PoR was not explained by tree seeds or  
240 berries (hereafter terrestrial non-frugivores, 11 species, Table 1), and examined this group separately. The  
241 simplest model (*i.e.* the one with the fewest explanatory variables) within  $\Delta$ AIC-value of two (Burnham &  
242 Anderson 2002), when compared with the lowest value, was considered the most parsimonious and therefore the  
243 best model.

244 To achieve stationarity, we removed long-term trends from the dependent variable (PoR) and all  
245 explanatory variables. The trends were analysed as explained below (*Analysis of temporal trends*). We detrended  
246 the variables with the most complex model of a trend within  $\Delta$ AIC-value of two (Table S3, Table S4), because  
247 thereby we best ensured linearity between dependent and explanatory variables. Residuals from these detrending  
248 procedures were used in the analyses of inter-annual variation in PoR. All variables were also scaled to have an  
249 average of 0 and variation of 1. After the model selection procedure, we tested the best models for serial  
250 autocorrelation with a lag of 1 year. If significant autocorrelation was found, the data of the species in question  
251 was reanalysed with a generalized linear model with normally distributed errors and an autocorrelation  
252 parameter (corAR1 in package *nlme*) to examine whether including an autocorrelation parameter qualitatively  
253 altered the results.

254

## 255 *Analyses of temporal trends*

256 For each species, we used linear regressions to examine temporal trends over the study period (1987–2011) in  
257 temperatures, PoR, the components from which PoR was calculated (*i.e.* winter and summer abundances),  
258 breeding success, as well as spruce and birch and rowanberry crops. In addition, we also examined linear trends  
259 in PoR in three functional groups (waterbirds, terrestrial birds and terrestrial non-frugivores) using random-  
260 intercept mixed models with species as the random factor.

261 To account for multiple testing in all species-specific analyses, we applied false discovery rate method  
262 (FDR, Waite & Campbell 2006). We based our interpretation of whether an explanatory variable had an effect on  
263 dependent variable on the FDR-adjusted p-values and reported only them in the results (unadjusted p-values can  
264 be found in Tables S2–3). All analyses were made with R (version 3.1.0, R Core Team 2014).

265

## 266 **Results**

267 There was no trend in latitude of constant effort sites (linear regression,  $F_{1,676} = 1.928$ ,  $P = 0.17$ ), but the annual  
268 mean latitude of breeding waterbird census sites shifted significantly southwards ( $F_{1,23} = 5.44$ ,  $P = 0.029$ .  
269 However, this shift was only 57 kilometres in 25 years. The winter indices of species showed larger inter-annual  
270 variation than summer indices (mean CV 0.766 and 0.262,  $t = 4.852$ ,  $df = 26$ ,  $p < 0.001$ ; Fig S2; Table S1). In  
271 addition, winter indices had lower precision compared to summer indices (mean RSEs 45.8 % and 13.3 %,   
272 paired t-test  $t = -2.829$ ,  $df = 26$ ,  $p = 0.009$ ; Table S1)

273 Early-winter temperature had a positive relationship with the inter-annual variation in PoR in five  
274 waterbird species (mute swan *Cygnus olor*, whooper swan *Cygnus cygnus*, tufted duck *Aythya fuligula*,  
275 goosander *Mergus merganser* and herring gull *Larus argentatus*), waterbirds as a functional group and one  
276 terrestrial birds (common starling, Figs 2c & S1, Tables 1 & S2). High abundance of seeds and/or berries  
277 resulted in high PoR in seven terrestrial species (common blackbird, fieldfare, common starling, Eurasian siskin,

common redpoll, common crossbill and Eurasian bullfinch) and terrestrial species as a functional group (Fig. S1, Tables 1 & S2). Breeding success had a positive relationship with PoR only in yellowhammer *Emberiza citrinella* (Fig. S1, Tables 1 & S2). The previous winter's temperature did not explain PoR in any of the species. A significant (negative) autocorrelation was retained only in the best model of Eurasian bullfinch and the autocorrelation parameter had only a minor effect on the parameter values of the model (rowanberry:  $b = 0.682 \pm 0.166$ ,  $p < 0.001$ , FDR- $p = 0.007$ , autocorrelation parameter  $\phi = -0.517$ ).

During the 25-year study period, PoR increased in five waterbirds (mallard *Anas platyrhynchos*, tufted duck, common goldeneye *Bucephala clangula*, goosander and great black-backed gull *Larus marinus*), and in waterbirds as a group (Fig. S2, Tables 2 & S3). PoR decreased in one terrestrial species (greenfinch *Carduelis chloris*), but significant effect was not found either in group of terrestrial species or in terrestrial non-frugivores (Fig. S2, Tables 2 & S3). The model assuming non-linear trend in PoR was superior for great black-backed gull and in waterbirds as a group (Table S3). To make the between-species comparison easier, Table 2 only shows the linear models.

Seed and berry abundances (Fig. 1a), midwinter temperatures or early-winter temperatures showed no temporal trend during our study period (1987–2011; Fig. 1b, Table S4). Winter abundance increased in 12 species and decreased in 4 species; summer abundance increased in 10 species and decreased in 8 species (Table S5).

295

## 296 Discussion

This study provided the first multi-species overview of changes in PoR and relatedness of these changes to environmental factors in partially migratory animals. The findings suggest that direct plastic responses in relation to environmental fluctuation are more important explaining the inter-annual variation in PoR than evolutionary responses measured as delayed effect of the previous winter, but the increasing trend of PoR in waterbirds might have been caused by selective response to the lack of severe winters during the study period. In addition, the species of aquatic and terrestrial habitats differed from each other in both long-term trends in PoR and environmental factors causing the inter-annual variation in PoR. Furthermore, breeding success had hardly

304 any effect on PoR (one species out of 11).

305

### 306 *Direct plastic responses – impact of temperature*

307 We found that early-winter temperature explains the inter-annual variation in PoR in five of nine waterbird  
308 species. Winter temperature is highly correlated with the occurrence and extent of ice-cover in the Baltic Sea  
309 (Luomaranta *et al.* 2014), which is the most probable causal link between the early-winter temperature and PoR  
310 in waterbirds. The migration period of the waterbird species overlaps with the freezing of lakes and coastal areas  
311 of the Baltic Sea (Lehikoinen & Jaatinen 2012) and therefore the early-winter temperature can directly affect the  
312 migration decision and behaviour of individuals.

313 In contrast to waterbirds, the PoR of land bird species was generally not affected by temperature  
314 fluctuation (except common starling, out of 18 species). The most probable explanation for this is that food  
315 availability of these species is not strongly directly temperature related. Many of them either commonly exploit  
316 bird feeders (blue tit, great tit, chaffinch *Fringilla coelebs*, brambling, greenfinch, yellowhammer, Väisänen  
317 1994), or are urban dwellers (hooded crow *Corvus corone cornix* and jackdaw *Corvus monedula*, Jokimäki &  
318 Suhonen 1998). These species are, similar to frugivores, able to find enough food to survive even during the  
319 most severe winters (Hildén & Koskimies 1969). The lack of temperature effect in reed bunting *Emberiza*  
320 *schoeniclus* was probably due to its dependency on seed crop of Common Reed *Phragmites australis* (Matessi *et*  
321 *al.* 2002).

322

### 323 *Direct plastic responses – impact of seed and berry crop*

324 In our study, the PoR of 7 out of 18 terrestrial species was connected to tree seed crops. This was expected  
325 because it is well documented that migration of many frugivorous species depend on the annual crop (e.g. Fox *et*  
326 *al.* 2009). Because of the strong relationship between crops and PoR, we believe the lack of long-term trends in  
327 rowan, spruce or birch crops explain the lack of trends in PoR in these species (Wallenius 1999; Lindén *et al.*

2011). Furthermore, inter- or intra-specific food competition could affect the PoR of species. To understand this properly the food availability (including alternative food items) as well species-specific per capita consumption rates should be measured.

Some caution is necessary when interpreting the results as variation in proportion of residents, because we used count data of unmarked individuals and cannot know the proportion of the wintering individuals that originated outside Finland. Still, the interpretation should be rather robust because the relationships between temperature or seed crop and PoR were dominated by the variation in winter abundance, and it is probable that the response of wintering behaviour to environmental variation is similar regardless whether the individuals originate from inside or outside Finland.

#### *The increasing trend in PoR in waterbirds*

PoR had an increasing trend in waterbirds despite the lack of a respective positive trend in winter temperatures during the study period. The increase in PoR may have been caused by a longer-term climate warming which caused mean and minimum midwinter temperatures to remain at a higher level during the whole study period than in the previous decades (Luomaranta *et al.* 2014). This would have caused the extent of ice cover to remain below the threshold when it was on average beneficial to try to overwinter in Finland (Lehikoinen *et al.* 2013). During the colder winters, more individuals were forced to migrate south causing a decrease in PoR (Lehikoinen *et al.* 2013), but this apparently had no effect on the overall success of the strategy of trying to winter in Finland, because the proportion of individuals utilizing this strategy increased year after year and independently of previous winter's temperature.

Another potential explanation for the observed trends in waterbirds could be a shift of both wintering and breeding areas towards northeast-east. Such a shift of the whole distribution could increase wintering numbers and decrease breeding numbers, a pattern we found in tufted duck and goosander, which both have extended their winter range towards north-east (Lehikoinen *et al.* 2013). This would mean that no increase in the



353 real proportion of residents in the total population per se had occurred, but the apparent increase in PoR had been  
354 the consequence of observing proportionally more and more wintering individuals originating from outside  
355 Finnish borders. However, this is unlikely to be the whole explanation for the observed pattern in ducks, because  
356 female ducks are strongly philopatric but show less fidelity towards wintering sites, and therefore breeding  
357 distribution is expected to change much more slowly than wintering distribution (Guillemain *et al.* 2013).  
358 Therefore it is plausible that the increase in wintering abundance was mostly caused by changes in the migratory  
359 behaviour of the Finnish populations. Since the extent of ice cover in the Baltic Sea is expected to decrease  
360 dramatically during the next 100 years (Luomaranta *et al.* 2014), we expect the wintering abundances and  
361 thereby PoR of waterbirds continue to increase in Finland, but likely also in other high latitude regions.

362

#### 363 *Selective responses - impact of previous winter's temperature*

364 We found no effect of previous winter's temperature on PoR in any species, which implies that the migration of  
365 partial-migrants would be more of a plastic and opportunistic behaviour than a result of temperature related  
366 survival of resident individuals. On the other hand, the long-term increase in PoR in waterbirds could had been  
367 caused by higher survival of residents causing either a selective or learned response for increased residency.  
368 Whether winter temperatures remaining above some threshold was the key for successful wintering and hence  
369 the increasing trend in PoR remains unknown, because such an effect is impossible to detect with analyses if the  
370 study period does not include winters cold enough to decrease the overwintering success.

371         The optimal migration decision of an individual could be affected by genetic inclination, social status,  
372 physiological condition, environmental conditions, population density or frequency of the two migration  
373 strategies (Taylor & Norris 2007; Kokko 2011). For example, a cold winter could cause poor survival of  
374 residents after which, assuming frequency-dependent response, the optimal strategy for some individuals from  
375 the migratory proportion could be to change their migration strategy and become residents. This kind of  
376 mechanism might counterbalance the effect of lower resident survival on PoR and thereby remove the effect of  
377 previous winter's temperature. Moreover, if cold temperature-induced poor winter survival leads to a decrease in  
378 summer abundance, it makes observing the potential decrease in PoR difficult because both the numerator and

denominator in our PoR calculation are reduced. This is mainly a concern in the species in which a substantial part of the population overwinters in Finland and winter survival is affected by the temperature, like goldcrest and Eurasian treecreeper (Hildén & Koskimies 1969). Furthermore, in several species either early-winter temperature or tree crops affected PoR so strongly that that they could have masked the possible effect of the previous winter. In conclusion, the chances of detecting subtle effects of previous year's temperature on PoR were not very high. Nonetheless, we can conclude that the effect of previous winter's temperature on the inter-annual variation in PoR was smaller than the direct effect of the environmental conditions just before a winter. A study following individuals for multiple years would be needed to conclusively find out the relative importance of innate mechanisms and environmental forcing on migration decisions.

388

#### *The differences between waterbirds and terrestrial birds*

In several terrestrial species PoR did not change despite winter abundance increased, because summer abundance increased at an equal rate. This suggests migration remained the optimal strategy for a similar proportion of individuals as before. All these species are feeder exploiters whose winter food availability improved as bird feeding became more common during the study period (Väisänen 2008), so improved winter survival rate of residents leading to an increase in PoR would had been expected. A potential explanation for the lack of increase in PoR is that birth rate increased equally to the increase in winter survival of residents (Griswold, Taylor & Norris 2011), possibly because improved pre-breeding condition of wintering residents allowed them to breed earlier and lay larger clutches. Another, not mutually exclusive explanation is that the increase in April temperatures during the study period (Lehikoinen et al. 2009) enabled individuals to breed earlier (Meller, Lehikoinen & Vähätalo 2013) and lengthened the breeding season increasing second breeding attempts (Halupka, Dyrz, & Borowiec, 2008). These mechanisms might have contributed to the decreasing trend in PoR found in greenfinch, but ultimately the reason for the observed decrease remains unknown.

Another possibility is that PoR actually increased in these species, but we failed to observe this with the methodology applied. If an increase in summer abundance was mostly caused by an increase in abundance of residents due to their improved winter survival, it would increase both numerator (winter abundance) and

denominator (summer abundance) in our PoR calculation and thereby mask part of the increase in PoR. The greater the proportion of resident individuals was at the beginning of the study period, the more potential there was for this methodological problem to affect our ability to detect changes in PoR. However, comparing the migration numbers (Lehikoinen *et al.* 2008) of the species with the most potential for a masked increase in PoR (great tit, blue tit and jackdaw) to the changes in breeding abundance shows that both increased at a similar rate during the study period. Thereby this alternative method for analysing changes in PoR (Nilsson *et al.* 2006) suggests that PoR indeed did not change in these species.

The higher variation of winter than summer indices means that in most species the variation in PoR was more affected by, and in some almost completely determined by, winter abundances. The lower precision of the winter indices, especially found in some waterbirds and frugivorous species, was caused by the high inter-annual variation in how individuals were distributed between the routes during the counts. This was probably due to flocking behaviour and mobile foraging strategies of opportunistically adjusting to spatiotemporal changes in food availability (Newton 1998). The relatively low precision of winter indices did not mask the strong relationships we found between the environmental variables and PoR, but it might have caused us not to detect more subtle connections.

Most of our study species have either different trends during summer and winter, or only a small proportion of individuals overwinter in Finland (Koskimies 1993). Therefore we are confident that if an overall change in PoR in all terrestrial species or non-frugivorous terrestrial species had occurred, we would have been able to detect it.

The dependence of waterbirds on non-frozen water is the most potential cause for the observed difference in sensitivity to the temperature between waterbirds and terrestrial species. The food of most terrestrial species wintering in Finland (seeds, berries, feeding sites and other anthropogenic food, dormant invertebrates) is only a little affected by changes in the winter temperature, while if ice covers all shallow waters, feeding becomes impossible for waterbirds. On the other hand, when temperature rises over a certain threshold, then the lack of ice may change the wintering possibilities of waterbirds abruptly from impossible to excellent, because the availability of their underwater food is dictated almost only by the existence of ice.

431           The occurrence of snow and frost below zero temperature decrease the success of feeding of many  
432 terrestrial species as well. Thus, most breeding birds, especially the species feeding on invertebrates, seldom or  
433 never try to winter in Finland. Therefore we do not state that the wintering of waterbirds would be generally  
434 more temperature dependent than terrestrial birds, even though the difference was clear in our study.  
435 Phylogenetical differences (all terrestrial birds were passerines) and smaller size of most terrestrial species in our  
436 study compared with waterbirds may also have contributed to the observed differences.

437

#### 438 **Acknowledgements**

439 Comments of three anonymous referees improved the clarity of the manuscript. Jenny and Antti Wihuri  
440 Foundation and Ella and Georg Ehrnrooth Foundation financed this work (grants for KM). AL has received  
441 funding from the Academy of Finland (grant number 275606). Special thanks to all volunteers and staff from the  
442 Finnish Museum of Natural History and Natural Resources Institute Finland who helped in either collecting or  
443 maintaining data. Finnish Ministry of Environment has economically supported Finnish winter and breeding bird  
444 censuses.

445

#### 446 **Data accessibility**

447 Data is archived in Dryad: doi:10.5061/dryad.js17t

448

#### 449 **References**

- 450 Adriaensen, F., Ulenaers, P. & Dhondt, A.A. (1993) Ringing recoveries and the increase in numbers of European  
451 Great Crested Grebe *Podiceps cristatus*. *Ardea*, **81**, 59–70.
- 452 Alerstam, T. (1990) *Bird Migration*. Cambridge University Press, Cambridge.
- 453 Baillie, S.R., Green, R.E., Boddy, M. & Buckland, S.T. (1986) *An Evaluation of the Constant Effort Site Scheme*.  
454 Norfolk, UK.
- 455 Berthold, P., Mohr, G. & Querner, U. (1990) Control and evolutionary potential of obligate partial migration

456 results of a two way selective breeding experiment with the blackcap *Sylvia atricapilla*. *Journal für*  
457 *Ornithologie*, **131**, 33–46.

458 Berthold, P. (2001) *Bird Migration: a General Survey*. Oxford University Press, Oxford.

459 Brommer, J.E., Lehikoinen, A. & Valkama, J. (2012) The Breeding Ranges of Central European and Arctic Bird  
460 Species Move Poleward. *PloS one*, **7(9)**: e43648.

461 Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: a Practical Information-*  
462 *theoretic Approach*, 2nd ed. Springer, USA.

463 Fox, A.D., Kopro, S., Lehikoinen, A., Lyngs, P. & Väisänen, R.A. (2009) Northern Bullfinch *Pyrrhula p.*  
464 *pyrrhula* irruptive behaviour linked to rowanberry *Sorbus aucuparia* abundance. *Ornis Fennica*, **86**, 51–60.

465 Fraixedas, S., Lehikoinen, A. & Lindén, A. (2015) Impacts of climate and land-use on wintering bird populations  
466 in Finland. *Journal of Avian Biology*, **46**, 63–72.

467 Gregory, R.D., Van Strien, A., Vorisek, P., Gmelig Meyling, A.W., Noble, D.G., Foppen, R.P.B. & Gibbons, D.W.  
468 (2005) Developing indicators for European birds. *Philosophical transactions of the Royal Society of*  
469 *London. Series B, Biological sciences*, **360**, 269–88.

470 Griswold, C.K., Taylor, C.M. & Norris, D.R. (2011) The equilibrium population size of a partially migratory  
471 population and its response to environmental change. *Oikos*, **120**, 1847–1859.

472 Guillemain, M., Pöysä, H., Fox, A.D., Arzel, C., Dessborn, L., Ekroos, J., Gunnarsson, G., Holm, T.E.,  
473 Christensen, T.K., Lehikoinen, A., Mitchell, C., Rintala, J. & Møller, A.P. (2013) Effects of climate change  
474 on European ducks : what do we know and what do we need to know? *Wildlife Biology*, **19**, 1–16.

475 Haila, Y., Tiainen, J. & Vepsäläinen, K. (1986) Delayed autumn migration as an adaptive strategy of birds in  
476 northern Europe: evidence from Finland. *Ornis Fennica*, **63**, 1–9.

477 Halupka, L., Dyrce, A., & Borowiec, M. (2008). Climate change affects breeding of reed warblers *Acrocephalus*  
478 *scirpaceus*. *Journal of Avian Biology*, **39**, 95–100.

479 Hario, M. & Rintala, J. (2011) Population trends of the archipelago birds along Finnish coasts during 1986–2010

480 (in Finnish with English summary). *Linnut-vuosikirja 2010*, **40**–51.  
 481 Hebblewhite, M. & Merrill, E.H. (2011) Demographic balancing of migrant and resident elk in a partially  
 482 migratory population through forage-predation tradeoffs. *Oikos*, **120**, 1860–1870.  
 483 Hildén, O. & Koskimies, J. (1969) Effects of the Severe Winter of 1965/66 upon Winter Bird Fauna in Finland.  
 484 *Ornis Fennica*, **46**, 22–31.  
 485 Hokkanen, T. (2000) Seed crops and seed crop forecasts for a number of tree species. In: Mälkönen, E., Babich,  
 486 N.A., Krutov, V.I. & Markova, I.A. (eds.). Forest Regeneration in the Northern Parts of Europe. *The*  
 487 *Finnish Forest Research Institute, Research Papers*, **790**, 87–97.  
 488 IPCC, Van Oldenborgh, G.J., Collins, M., Arblaster, J., Christensen, J.H., Marotzke, J., Power, S.B.,  
 489 Rummukainen, M. & Zhou, T. (eds) (2013) *Annex I: Atlas of Global and Regional Climate Projections. In:*  
 490 *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth*  
 491 *Assessment Report of the Intergovernmental Panel on Climate Change*.  
 492 Jokimäki, J. & Suhonen, J. (1998) Distribution and habitat selection of wintering birds in urban environments.  
 493 *Landscape and Urban Planning*, **39**, 253–263.  
 494 Kaitala, A., Kaitala, V. & Lundberg, P. (1993) A Theory of Partial Migration. *The American Naturalist*, **142**, 59–  
 495 81.  
 496 Kokko, H. (2011) Directions in modelling partial migration: how adaptation can cause a population decline and  
 497 why the rules of territory acquisition matter. *Oikos*, **120**, 1826–1837.  
 498 Koskimies, P. (1993) Population sizes and recent trends of breeding and wintering birds in Finland (in Finnish  
 499 with English summary). *Linnut*, **28**, 6–15.  
 500 Koskimies, P. & Väisänen, R.A. (1991) *Monitoring Bird Populations - A Manual of Methods Applied in Finland*.  
 501 Uusikaupunki.  
 502 Lehikoinen, A. (2013) Climate change, phenology and species detectability in a monitoring scheme. *Population*  
 503 *Ecology*, **55**, 315–323.

504 Lehtikoinen, A., Ekroos, J., Jaatinen, K., Lehtikoinen, P., Lindén, A., Piha, M., Vattulainen, A. & Vähätalo, A.V.  
 505 (2008) Bird population trends based on the data of Hanko Bird Observatory (Finland) during 1979-2007 (in  
 506 Finnish with English summary). *Tringa*, **35**: 146–209.

507 Lehtikoinen, A. & Jaatinen, K. (2012) Delayed autumn migration in northern European waterfowl. *Journal of*  
 508 *Ornithology*, **153**, 563–570.

509 Lehtikoinen, A., Jaatinen, K., Vähätalo, A. V, Clausen, P., Crowe, O., Deceuninck, B., Hearn, R., Holt, C.A.,  
 510 Hornman, M., Keller, V., Nilsson, L., Langendoen, T., Tománková, I., Wahl, J. & Fox, A.D. (2013) Rapid  
 511 climate driven shifts in wintering distributions of three common waterbird species. *Global Change Biology*  
 512 **19**, 2071–2081.

513 Lehtikoinen, A., Väisänen, R.A. & Hokkanen, T. (2010) Variation of abundance in 14 bird species in relation to  
 514 the seed and berry crop of trees in Finland in winters 1957-2009 (in Finnish with English summary).  
 515 *Linnut-vuosikirja* **2009**, 90–99.

516 Lindén, A., Lehtikoinen, A., Hokkanen, T. & Väisänen, R. A. (2011) Modelling irruptions and population  
 517 dynamics of the great spotted woodpecker - joint effects of density and cone crops. *Oikos*, **120**, 1065–1075.

518 Love, O.P., Gilchrist, H.G., Descamps, S., Semeniuk, C.A.D. & Bêty, J. (2010) Pre-laying climatic cues can time  
 519 reproduction to optimally match offspring hatching and ice conditions in an Arctic marine bird. *Global*  
 520 *Change Biology*, **164**, 277–286.

521 Luomaranta, A., Ruosteenoja, K., Jylhä, K., Gregow, H., Haapala, J. & Laaksonen, A. (2014) Multimodel  
 522 estimates of the changes in the Baltic Sea ice cover during the present century. *Tellus*, **66**, 22617.

523 Matessi, G., Griggio, M., Pilastro, A., Biologia, D., Padova, U. & Bassi, U.B. (2002) The geographical  
 524 distribution of populations of the large-billed subspecies of reed bunting matches that of its main winter  
 525 food. *Biological Journal of the Linnean Society*, **75**, 21–26.

526 Newton, I. (1998) Population limitation in birds. Academic, London.

527 Newton, I. & Dale, L. (1996) Relationship Between Migration and Latitude Among West European Birds.  
 528 *Journal of Animal Ecology*, **65**, 137–146.

529 Nilsson, A.L.K., Lindström, Å., Jonzén, N., Nilsson, S.G. & Karlsson, L. (2006) The effect of climate change on  
530 partial migration? the blue tit paradox. *Global Change Biology*, **12**, 2014–2022.

531 Pannekoek, J. & Van Strien, A. J. (2005) TRIM 3 manual. Trends and indices for monitoring data. CBS,  
532 Statistics Netherlands, Voorburg, Netherlands.

533 Parmesan, C. (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology,*  
534 *Evolution, and Systematics*, **37**, 637–669.

535 Piha, M. & Haapala, J. (2012) Constant Effort Sites in Finland: Population and productivity indices 1987-2011  
536 (in Finnish with English summary). *Linnut-vuosikirja* **2011**, 82–87.

537 Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R Core Team. (2014) nlme: Linear and Nonlinear Mixed  
538 Effects Models. R package version 3.1-117.

539 Pulido, F. (2011) Evolutionary genetics of partial migration - the threshold model of migration revis(it)ed. *Oikos*,  
540 **120**, 1776–1783.

541 Pöysä, H., Rintala, J., Lehikoinen, A., & Väisänen, R.A. (2013) The importance of hunting pressure, habitat  
542 preference and life history for population trends of breeding waterbirds in Finland. *European Journal of*  
543 *Wildlife Research*, **59**, 245–256.

544 R Core Team. (2014) R: A language and environment for statistical computing.

545 Reinikainen, A. (1937) The irregular migrations of the Crossbill, *Loxia c. curvirostra*, and their relation to the  
546 cone-crop of the Conifers. *Ornis Fennica*, **14**, 55–64.

547 Robinson, R.A., Baillie, S.R. & Crick, H.Q.P. (2007) Weather-dependent survival: implications of climate  
548 change for passerine population processes. *Ibis*, **149**, 357–364.

549 Robinson, R.A., Freeman, S.N., Balmer, D.E. & Grantham, M.J. (2007) Cetti's Warbler *Cettia cetti*: analysis of  
550 an expanding population: Capsule Productivity in the UK Cetti's Warbler population is constant, but  
551 overwinter survival has become increasingly dependent on winter temperatures. *Bird Study*, **54**, 230–235.

552 Saurola, P., Valkama, J. & Velmala, J. (2013) The Finnish Bird Ringing Atlas. Vol. 1. Finnish Museum of Natural



553 History and Finnish Ministry of Environment.

554 Sillett, T.S. & Holmes, R.T. (2002) Variation in Survivorship of a Migratory Songbird throughout Its Annual  
555 Cycle. *Journal of Animal Ecology*, **71**, 296–308.

556 Taylor, C.M. & Norris, D.R. (2007) Predicting conditions for migration: effects of density dependence and  
557 habitat quality. *Biology letters*, **3**, 280–283.

558 Terrill, S.B. & Able, K.B. (1988) Bird Migration Terminology. *The Auk*, **105**, 205–206.

559 Valkama, J., Saurola, P., Lehtikainen, A., Lehtikainen, E., Piha, M., Sola, P. & Velmala, W. (2014) The Finnish  
560 Bird Ringing Atlas. Vol. 2. Finnish Museum of Natural History and Finnish Ministry of Environment.

561 Venäläinen, A., Tuomenvirta, H., Pirinen, P. & Drebs, A. (2005) A Basic Finnish Climate Data Set 1961-2000 -  
562 Description and Illustrations. *Reports ↓ Finnish Meteorological Institute*.

563 Visser, M.E., Perdeck, A.C., Van Balen, J.H. & Both, C. (2009) Climate change leads to decreasing bird  
564 migration distances. *Global Change Biology*, **15**, 1859–1865.

565 Vliet, J. Van, Musters, C.J.M. & Keurs, J. Ter. (2009) Changes in migration behaviour of Blackbirds *Turdus*  
566 *merula* from the Netherlands. *Bird Study*, **56**, 276–281.

567 Väisänen, R.A. (1994) Abundance of the 58 most common bird species at winter feeding sites in Finland (in  
568 Finnish with English summary). *Linnut*, **29**, 16–23.

569 Väisänen, R.A. (2003) Regional population trends of 33 common bird species in Finland during 27 winters (in  
570 Finnish with English summary). *Linnut-vuosikirja*, **2002**, 60–79.

571 Väisänen, R.A. (2008) Changes in frequency and abundance of 63 bird species at winter feeding sites in Finland  
572 during 19 winters 1998/1989-2006/2007 (in Finnish with English summary). *Linnut-vuosikirja*, **2007**, 60–  
573 79.

574 Väisänen, R.A., Lammi, E. & Koskimies, P. (1998) Distribution, numbers and population changes of Finnish  
575 breeding birds (Muuttuva pesimälinnusto). Otavan kirjapaino, Keuruu.

576 Waite, T.A. & Campbell, L.G. (2006) Controlling the false discovery rate and increasing statistical power in

577 ecological studies. *Ecoscience*, **13**, 439–442.

578 Wallenius, T.H. (1999) Yield variations of some common wild berries in Finland in 1956 – 1996. *Annales*

579 *Botanici Fennici*, **36**, 299–314.

580

581

582    **Supporting Information**

583    The following Supporting Information is available for this article online

584    Table S1. Annual sample sizes of bird censuses.

585    Table S2. All models explaining the annual variation in PoR.

586    Table S3. All models of trends in PoR.

587    Table S4. All models of trends in tree crops and winter temperatures.

588    Table S5. Trends in winter and summer abundances.

589    Fig. S1. All significant effects the explanatory variables on annual PoR.

590    Fig. S2. The annual indices of the winter abundance, summer abundance and PoR.

591

592 Table 1. The best models, according to a model selection process, for explaining the inter-annual variation in  
593 proportion of residents (PoR) in 27 partially migratory bird species, and waterbirds (W), all terrestrial birds (T)  
594 and terrestrial non-frugivorous (T nf) birds as groups. CES denotes whether constant effort site data for  
595 calculating a breeding success index was available and used in the model selection process of a species. The  
596 species-specific p-values are adjusted for false discovery rate. See text and Table S2 for details.

Species	n	Group	CES	r <sup>2</sup>	The best model	b ± SE	p
Waterbirds	225	W	no	–	Early-winter temperature	0.47 ± 0.06	<0.001
Terrestrial birds	450	T	no	–	Tree seed & berry crop	0.37 ± 0.04	<0.001
Terrestrial non-frugivores	275	T nf	no	–	Null model	–	–
Mute swan	25	W	no	0.44	Early-winter temperature	0.66 ± 0.16	0.005
Whooper swan	25	W	no	0.56	Early-winter temperature	0.75 ± 0.14	<0.001
Mallard	25	W	no	–	Null model	–	–
Tufted duck	25	W	no	0.33	Early-winter temperature	0.57 ± 0.17	0.033
Common goldeneye	25	W	no	–	Null model	–	–
Goosander	25	W	no	0.50	Early-winter temperature	0.71 ± 0.15	0.002
Mew gull	25	W	no	0.26	Early-winter temperature	0.51 ± 0.18	0.090
Herring gull	25	W	no	0.36	Early-winter temperature	0.60 ± 0.17	0.019
Great black-backed gull	25	W	no	–	Null model	–	–
Common blackbird	24	T	yes	0.68	Tree seed or berry crop	0.83 ± 0.12	<0.001
Fieldfare	24	T	yes	0.84	Tree seed or berry crop	0.92 ± 0.08	<0.001
Goldcrest	25	T nf	no	0.23	Tree seed or berry crop	0.48 ± 0.18	0.119
Blue tit	24	T nf	yes	0.41	Previous winter's temperature	0.39 ± 0.17	0.243
					Breeding success	0.43 ± 0.17	0.158
Great tit	24	T nf	yes	–	Null model	–	–
Eurasian treecreeper	24	T nf	yes	–	Null model	–	–
Jackdaw	25	T nf	no	–	Null model	–	–
Hooded crow	25	T nf	no	–	Null model	–	–
Common starling	25	T	no	0.68	Tree seed or berry crop	0.49 ± 0.13	0.010
					Previous winter's temperature	0.35 ± 0.13	0.101
					Early-winter temperature	0.54 ± 0.12	0.004
Chaffinch	24	T nf	yes	0.43	Tree seed or berry crop	0.52 ± 0.17	0.054
					Previous winter's temperature	-0.47 ± 0.17	0.097
Brambling	25	T nf	no	0.25	Tree seed or berry crop	0.50 ± 0.18	0.094
Greenfinch	24	T nf	yes	–	Null model	–	–
Eurasian siskin	24	T	yes	0.73	Tree seed or berry crop	0.86 ± 0.11	<0.001
Common redpoll	25	T	no	0.65	Tree seed or berry crop	0.76 ± 0.13	<0.001
					Previous winter's temperature	0.29 ± 0.13	0.220
Common crossbill	25	T	no	0.62	Tree seed or berry crop	0.79 ± 0.13	<0.001
Eurasian bullfinch	24	T	yes	0.55	Tree seed or berry crop	0.74 ± 0.14	0.001

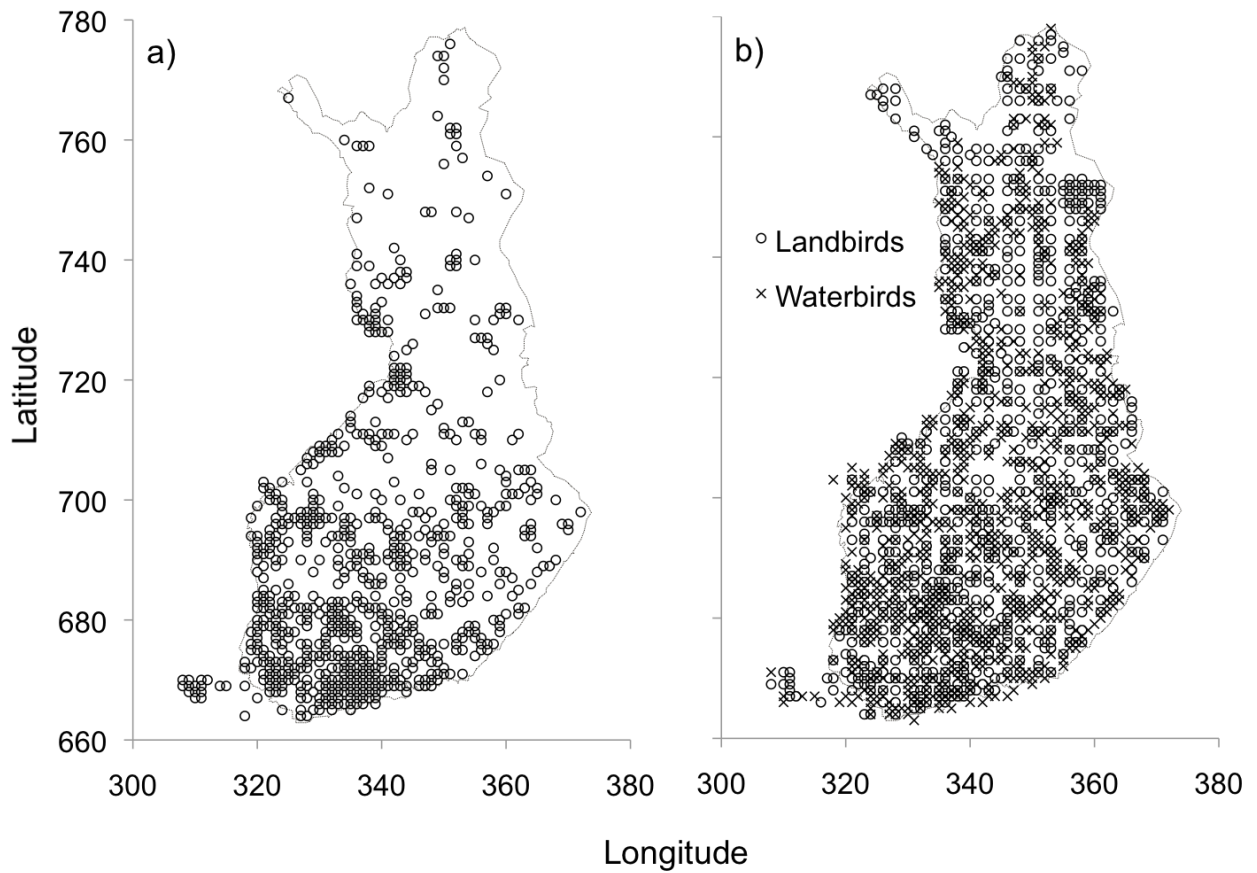
Yellowhammer	24	T nf	yes	0.58	Breeding success	$0.76 \pm 0.14$	<0.001
Reed bunting	24	T nf	yes	–	Null model	–	–

597 Table 2. Trends in proportion of residents (PoR) in 27 partially migratory bird species, and in waterbirds (W), all  
598 terrestrial birds (T) and terrestrial non-frugivorous birds (T nf) as groups. The change in PoR during the study  
599 period is presented as a percentage change from 1987 to 2011. The species-specific p-values are adjusted for  
600 false discovery rate.

Species	Group	r <sup>2</sup>	Trend	b ± SE	p
Waterbirds	W	–	Increase (+342%)	0.027 ± 0.004	<0.001
Terrestrial birds, all	T	–	No change	-0.001 ± 0.003	0.769
Terrestrial birds, non-frugivores	T nf	–	No change	-0.001 ± 0.002	0.612
Mute swan	W	0.19	No change	-0.013 ± 0.006	0.135
Whooper swan	W	0.07	No change	-0.012 ± 0.009	0.432
Mallard	W	0.44	Increase (+55%)	0.008 ± 0.002	0.003
Tufted duck	W	0.68	Increase (+33590%)	0.105 ± 0.015	<0.001
Common goldeneye	W	0.92	Increase (+4895%)	0.071 ± 0.004	<0.001
Goosander	W	0.60	Increase (+364%)	0.028 ± 0.005	<0.001
Mew gull	W	0.01	No change	0.007 ± 0.012	0.810
Herring gull	W	0.12	No change	0.020 ± 0.011	0.281
Great black-backed gull	W	0.41	Increase (+580%)	0.029 ± 0.007	0.005
Common blackbird	T	0.06	No change	0.010 ± 0.008	0.442
Fieldfare	T	0.00	No change	-0.003 ± 0.033	0.999
Goldcrest	T nf	0.07	No change	-0.005 ± 0.004	0.442
Blue tit	T nf	0.10	No change	0.003 ± 0.002	0.326
Great tit	T nf	0.15	No change	-0.004 ± 0.002	0.224
Eurasian treecreeper	T nf	0.07	No change	-0.003 ± 0.003	0.442
Jackdaw	T nf	0.00	No change	-0.000 ± 0.004	0.999
Hooded crow	T nf	0.10	No change	0.002 ± 0.001	0.327
Common starling	T	0.03	No change	-0.014 ± 0.016	0.658
Chaffinch	T nf	0.00	No change	0.001 ± 0.008	0.999
Brambling	T nf	0.00	No change	-0.000 ± 0.013	0.999
Greenfinch	T nf	0.34	Decrease (-39%)	-0.009 ± 0.003	0.018
Eurasian siskin	T	0.04	No change	0.018 ± 0.020	0.658
Common redpoll	T	0.00	No change	-0.001 ± 0.014	0.999
Common crossbill	T	0.00	No change	-0.004 ± 0.023	0.987
Eurasian bullfinch	T	0.12	No change	-0.011 ± 0.006	0.307
Yellowhammer	T nf	0.09	No change	-0.003 ± 0.002	0.380
Reed bunting	T nf	0.01	No change	0.008 ± 0.016	0.810

601

602



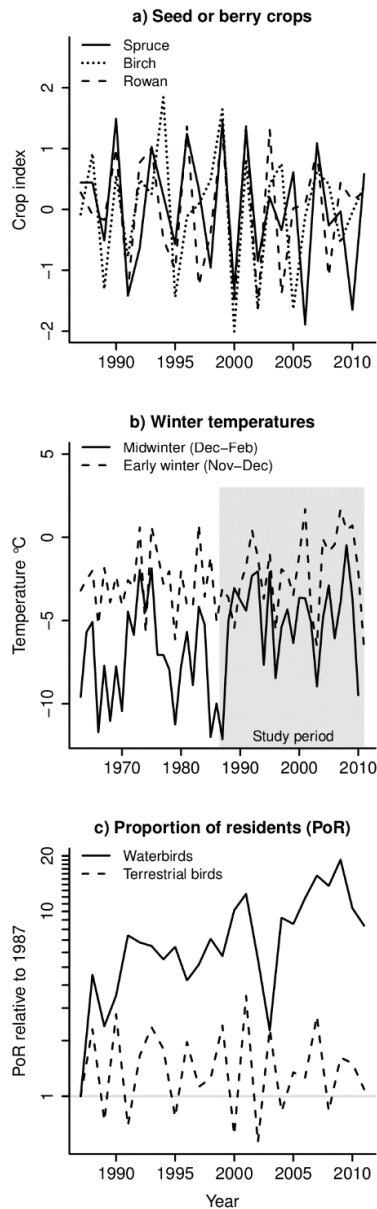
603

604 Figure 1. Spatial distribution of a) winter and b) summer count sites in Finnish uniform coordinate system during  
 605 1987–2011 and 1986–2010, respectively. The northern part of the country is less intensively covered during the  
 606 winter time because of very low bird densities and low amount of day light (sun does not rise above the horizon  
 607 in northern part of the country during winter bird count period). Winter bird counts are covering both waterbirds  
 608 and land birds simultaneously, which why census sites are shown only using one symbol.

609

610

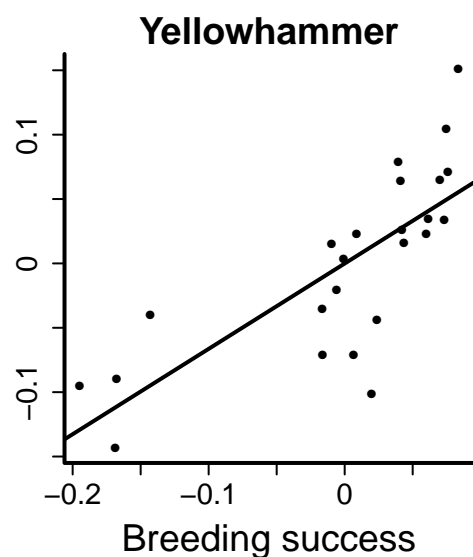
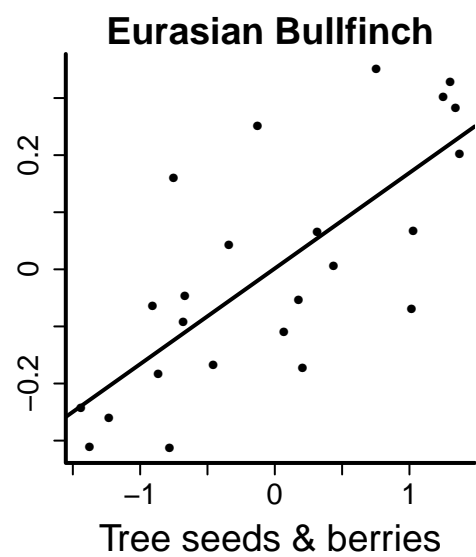
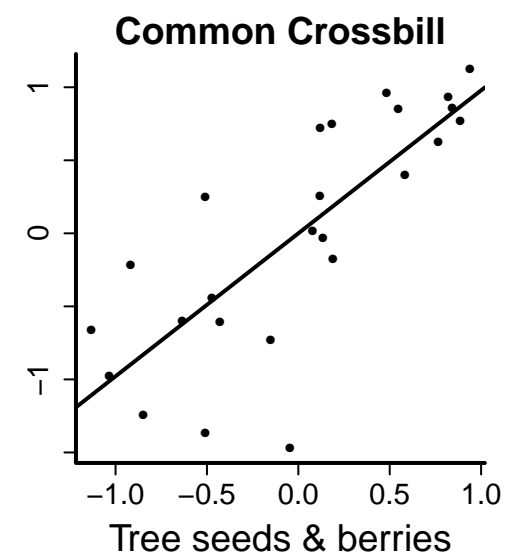
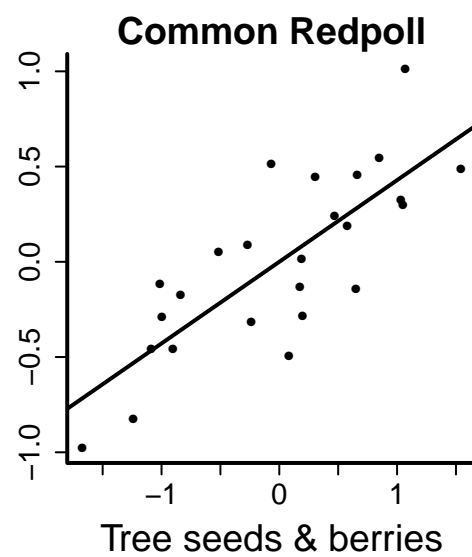
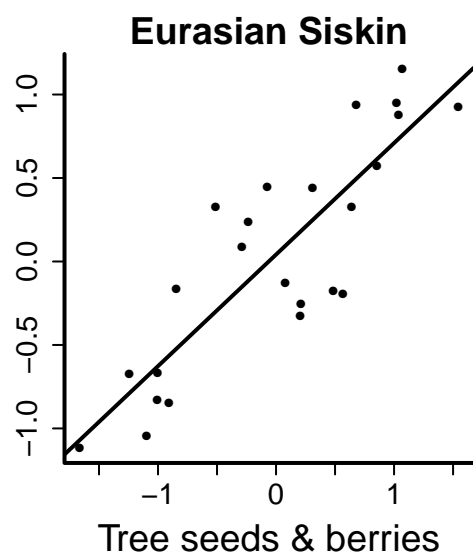
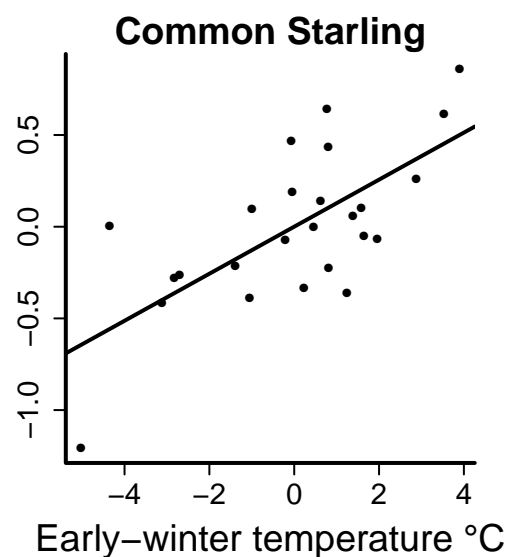
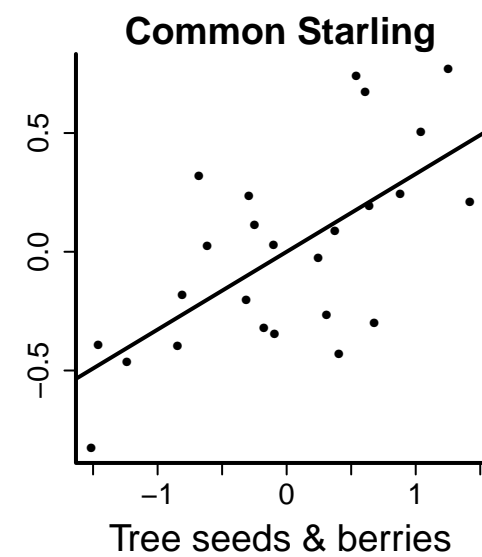
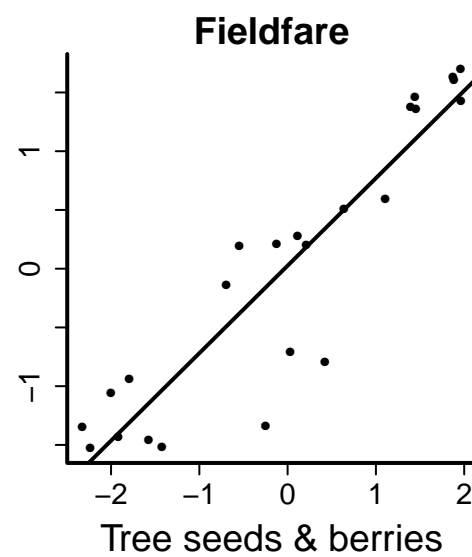
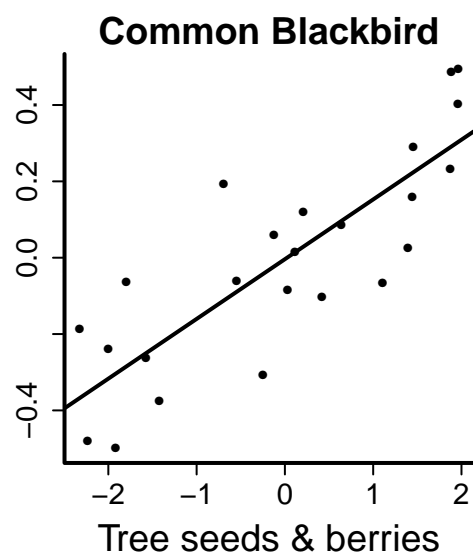
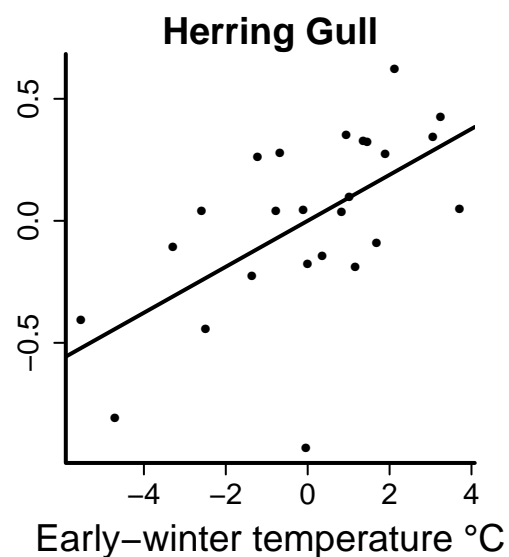
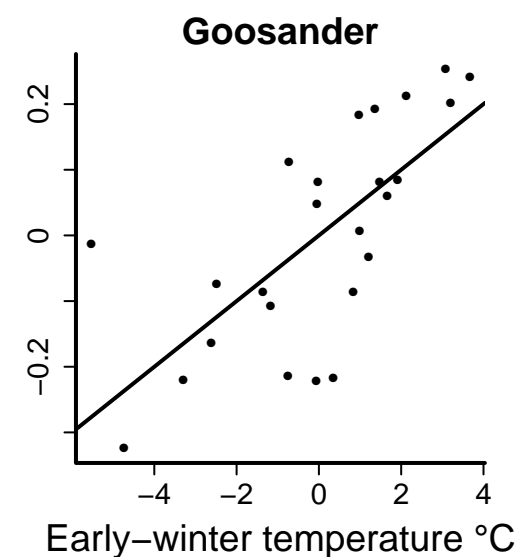
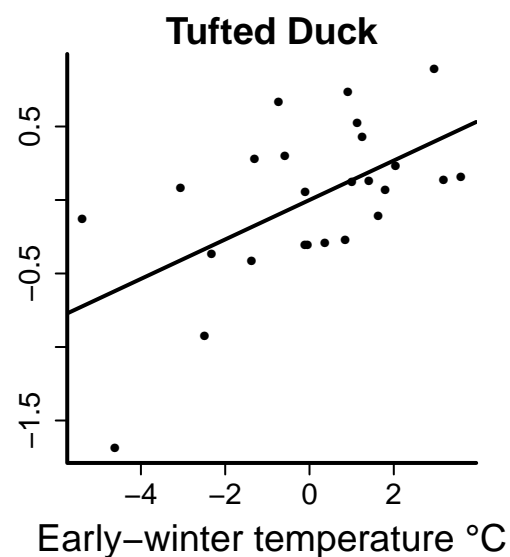
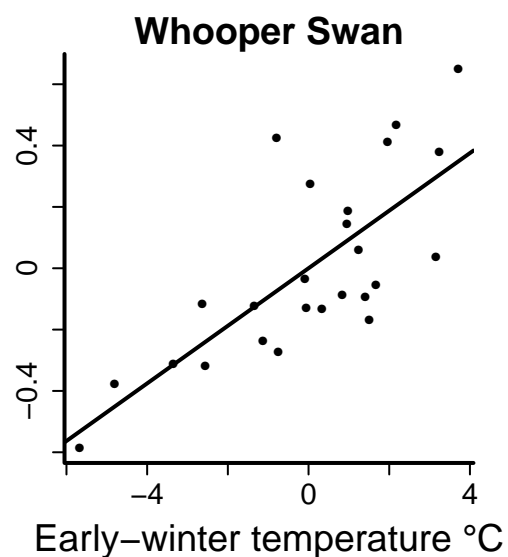
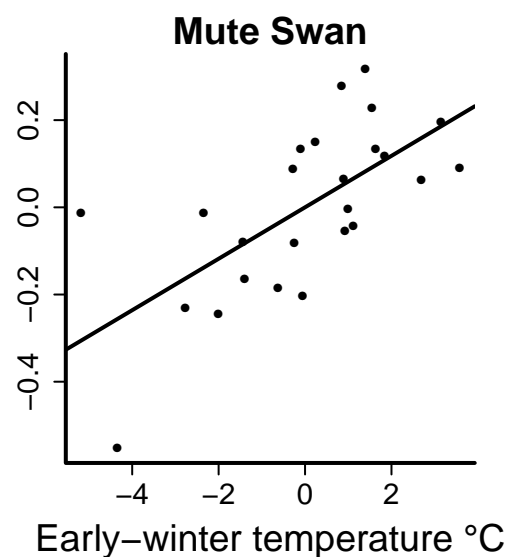
611



612

613 Figure 2. a) The annual seed crop index of spruce (solid line) and birch (dotted line), and annual berry crop index  
 614 of rowan (dashed line). All crop indices are scaled to have a mean of 0 and variance of 1. b) Annual early-winter  
 615 (November – December, dashed line) and midwinter (December – February, solid line) temperatures in Finland  
 616 during 1963–2011. The study period is shadowed. c) The annual means of proportions of residents (PoR)  
 617 compared with the first year of the study period (1987) in nine waterbirds (solid line) and 21 terrestrial birds  
 618 (dashed line). The years 1961–1986 were included to illustrate the lack of severe winters during the study period.





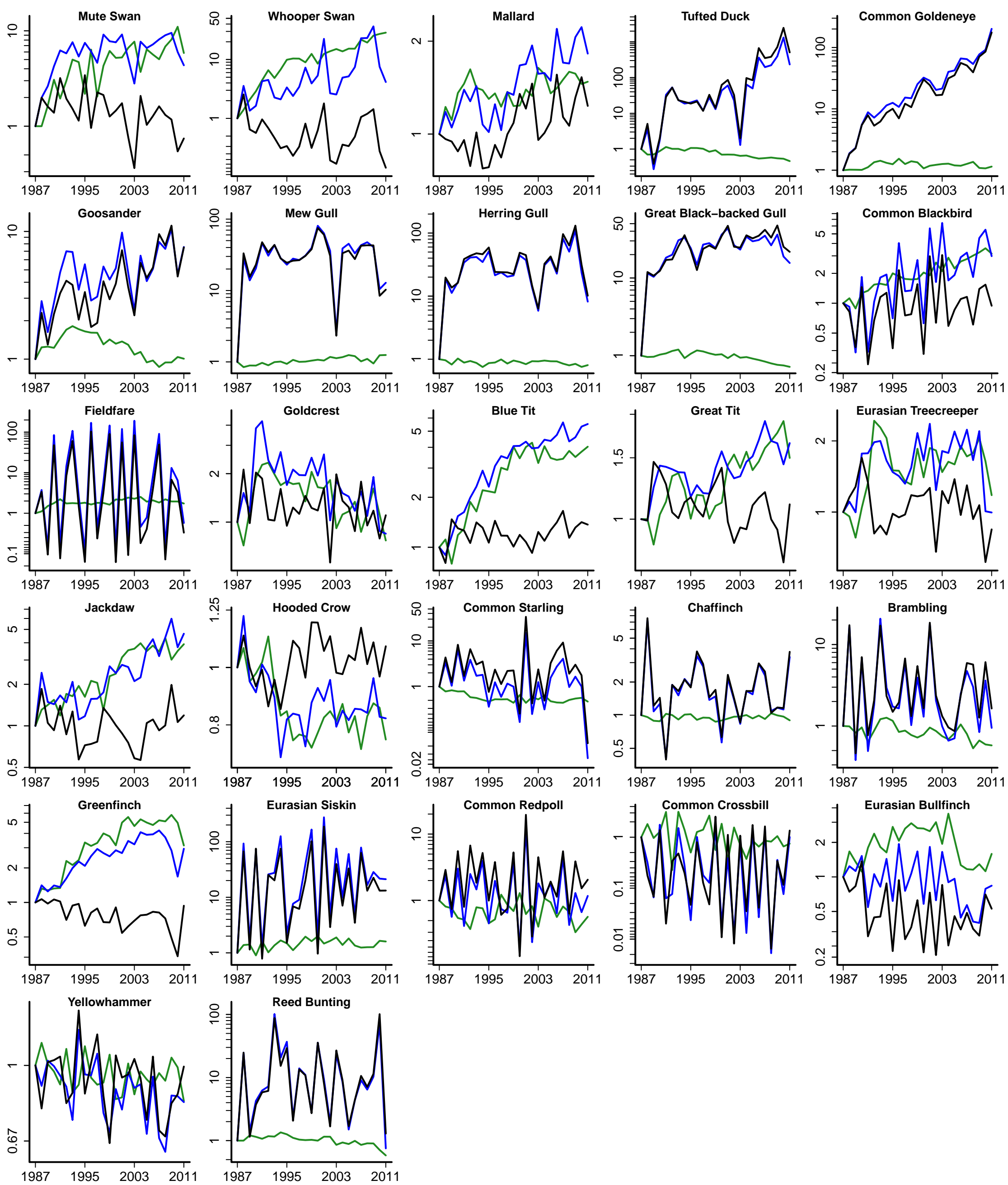


Table S1. Annual sample sizes (mean, min-max) in winter censuses (individuals), breeding censuses (pairs) and constant censuses (pairs) and constant effort site scheme (CES, individuals), as well as coefficients of variation (CV) and means of the annual relative standard errors (RSE) for winter and summer censuses during the 25-year study period (1987–2011).

Species	Winter census					Summer census					CES-scheme		
	Mean	Min	Max	CV	RSE	Mean	Min	Max	CV	RSE	Mean	Min	Max
Mute Swan	881	130	1518	0.34	27.4	195	28	504	0.48	11.7	—	—	—
Whooper Swan	462	43	2642	1.17	43.3	78	0	154	0.62	44.8	—	—	—
Mallard	8835	5027	13700	0.24	9.7	1102	871	1633	0.10	9.7	—	—	—
Tufted duck	4203	9	43471	2.08	233.0	1323	202	2923	0.27	7.4	—	—	—
Common Goldeneye	2311	77	13551	1.20	65.8	1580	1008	2375	0.11	9.3	—	—	—
Goosander	2482	408	5458	0.44	32.5	487	95	1003	0.22	10.7	—	—	—
Mew Gull	1417	40	3508	0.50	87.6	5725	381	9807	0.11	5.4	—	—	—
Herring Gull	6948	190	28102	0.70	62.2	8029	20	12529	0.08	6.1	—	—	—
Great Black-backed Gull	447	30	719	0.35	64.5	470	190	800	0.14	29.8	—	—	—
Common Blackbird	1099	139	2726	0.72	9.8	403	206	899	0.35	11.2	91	31	194
Fieldfare	12480	36	58270	1.55	67.8	1106	612	1767	0.16	7.6	104	35	149
Goldcrest	3009	1366	7294	0.44	7.0	364	185	759	0.31	11.2	—	—	—
Blue Tit	13540	3672	24081	0.39	5.5	232	95	502	0.38	15.3	314	25	602
Great Tit	28979	21308	41976	0.15	2.8	766	306	1581	0.21	6.7	439	153	719
Eurasian Treecreeper	431	236	637	0.25	9.8	78	33	177	0.25	23.1	9	2	20
Jackdaw	8259	3162	19818	0.49	12.9	161	38	368	0.40	22.1	—	—	—
Hooded Crow	12901	9704	19468	0.12	4.8	663	376	1213	0.13	6.8	—	—	—
Common Starling	82	0	707	1.40	72.0	125	59	230	0.21	18.8	—	—	—
Chaffinch	230	45	853	0.72	18.9	5123	2960	9496	0.05	3.1	277	170	437
Brambling	182	17	1034	1.34	46.9	1121	379	3512	0.23	8.0	—	—	—
Greenfinch	20919	7896	37716	0.35	6.9	309	101	838	0.41	15.8	207	49	554
Eurasian Siskin	3157	61	17604	1.33	77.2	1115	609	1964	0.19	7.8	163	40	482
Common Redpoll	13920	1368	82358	1.25	14.9	354	125	930	0.36	15.2	—	—	—
Common Crossbill	932	9	3412	1.16	28.5	391	58	812	0.68	18.2	—	—	—
Eurasian Bullfinch	7654	3269	14375	0.47	5.4	172	95	292	0.35	15.6	39	4	86
Yellowhammer	30544	21846	42403	0.15	5.2	690	355	1304	0.09	6.9	72	28	153
Reed Bunting	26	1	193	1.39	215.4	254	128	399	0.17	10.7	344	159	630



Table S2. All models explaining the annual variation in the proportion of birds that are not shown. Both unadjusted (p) and false discovery rate adjusted (FDR-p) p-values are shown. "ACF lag1" denotes serial autocorrelation with a lag of 1 and AICc is Akaike's information criterion (AICc). The best models (the simplest models) with  $\Delta AICc \leq 2$  are bolded

Species	Model	Intercept only (null model)	B	SE	t	p	FDR-p	df	r2	ACF lag1	AICc
Waterbirds	2	Early winter temperature	<b>0.473</b>	<b>0.059</b>	<b>8.020</b>	<b>&lt;0.001</b>	—	<b>215</b>	—	—	<b>588.1</b>
			0.138	0.068	2.080	0.039	—	215	—	—	640.3
Waterbirds	4	Tree seed & berry crop	0.095	0.065	-1.447	0.149	—	215	—	—	642.5
Waterbirds	6	Previous winter's temperature	0.464	0.059	7.865	<0.001	—	214	—	—	591.3
Waterbirds	6	Early winter temperature	-0.061	0.058	-1.044	0.297	—	214	—	—	592.8
Waterbirds	6	Tree seed & berry crop	0.469	0.059	7.922	<0.001	—	—	—	—	—
Waterbirds	7	Tree seed & berry crop	-0.174	0.065	-2.743	0.007	—	214	—	—	642.5
Waterbirds	7	Previous winter's temperature	0.153	0.067	2.259	0.023	—	—	—	—	—
Waterbirds	8	Tree seed & berry crop	-0.074	0.058	-1.276	0.203	—	213	—	—	594.9
Waterbirds	8	Previous winter's temperature	0.105	0.059	1.767	0.079	—	—	—	—	—
Waterbirds	8	Early winter temperature	0.458	0.059	7.736	<0.001	—	—	—	—	—
Terrestrial birds, all	1	Intercept only (null model)	—	—	—	—	—	432	—	—	1269.0
Terrestrial birds, all	2	Early winter temperature	0.017	0.047	0.356	0.722	—	431	—	—	1273.2
Terrestrial birds, all	2	Previous winter's temperature	0.082	0.047	1.742	0.082	—	431	—	—	1275.3
Terrestrial birds, all	4	Tree seed & berry crop	<b>0.374</b>	<b>0.044</b>	<b>8.529</b>	<b>&lt;0.001</b>	—	<b>431</b>	—	—	<b>1207.9</b>
Terrestrial birds, all	4	Previous winter's temperature	0.055	0.059	0.928	0.351	—	430	—	—	1278.5
Terrestrial birds, all	6	Tree seed & berry crop	0.008	0.047	0.162	0.871	—	—	—	—	—
Terrestrial birds, all	6	Early winter temperature	0.377	0.044	8.579	<0.001	—	430	—	—	1213.3
Terrestrial birds, all	6	Previous winter's temperature	0.044	0.044	0.999	0.318	—	—	—	—	—
Terrestrial birds, all	7	Tree seed & berry crop	0.359	0.044	8.359	<0.001	—	430	—	—	1213.6
Terrestrial birds, all	7	Previous winter's temperature	0.036	0.043	0.828	0.412	—	—	—	—	—
Terrestrial birds, all	8	Tree seed & berry crop	0.373	0.044	8.404	<0.001	—	429	—	—	1219.2
Terrestrial birds, all	8	Previous winter's temperature	0.032	0.045	0.709	0.479	—	—	—	—	—
Terrestrial birds, non-frugivores	8	Early winter temperature	0.004	0.044	0.904	0.368	—	—	—	—	—
Terrestrial birds, non-frugivores	2	Early winter temperature	0.021	0.061	0.351	0.726	—	263	—	—	784.7
Terrestrial birds, non-frugivores	2	Previous winter's temperature	-0.030	0.060	-0.502	0.616	—	263	—	—	784.6
Terrestrial birds, non-frugivores	4	Tree seed & berry crop	0.127	0.060	2.120	0.035	—	263	—	—	790.2
Terrestrial birds, non-frugivores	4	Previous winter's temperature	-0.033	0.061	-0.539	0.591	—	262	—	—	790.2
Terrestrial birds, non-frugivores	6	Tree seed & berry crop	0.025	0.061	0.409	0.683	—	—	—	—	—
Terrestrial birds, non-frugivores	6	Tree seed & berry crop	0.129	0.060	2.147	0.033	—	262	—	—	785.9
Terrestrial birds, non-frugivores	6	Early winter temperature	0.030	0.060	0.502	0.616	—	—	—	—	—
Terrestrial birds, non-frugivores	7	Tree seed & berry crop	0.133	0.061	2.197	0.029	—	262	—	—	785.0
Terrestrial birds, non-frugivores	7	Previous winter's temperature	-0.036	0.061	-0.592	0.553	—	—	—	—	—
Terrestrial birds, non-frugivores	8	Tree seed & berry crop	0.136	0.061	2.237	0.026	—	261	—	—	791.5
Terrestrial birds, non-frugivores	8	Previous winter's temperature	-0.051	0.061	-0.835	0.404	—	—	—	—	—
Terrestrial birds, non-frugivores	8	Early winter temperature	0.036	0.061	0.598	0.550	—	—	—	—	—
Mute Swan	1	Intercept only (null model)	—	—	—	—	—	23	—	-0.180	74.1
Mute Swan	2	Early winter temperature	<b>0.659</b>	<b>0.157</b>	<b>4.205</b>	<b>&lt;0.001</b>	<b>0.005</b>	<b>22</b>	<b>0.435</b>	<b>-0.192</b>	<b>62.2</b>
Mute Swan	2	Previous winter's temperature	-0.222	0.203	-1.092	0.268	0.919	22	0.049	-0.024	75.2
Mute Swan	4	Tree seed & berry crop	-0.264	0.201	-1.314	0.202	0.796	22	0.070	-0.128	74.7
Mute Swan	4	Previous winter's temperature	-0.259	0.150	-1.750	0.087	0.482	21	0.506	-0.331	61.4
Mute Swan	6	Tree seed & berry crop	-0.212	0.154	-1.370	0.184	0.758	21	0.479	-0.115	62.8
Mute Swan	6	Early winter temperature	0.642	0.154	4.157	<0.001	0.006	—	—	—	—
Mute Swan	7	Tree seed & berry crop	-0.240	0.203	-1.180	0.251	0.847	21	0.106	0.003	76.3
Mute Swan	7	Previous winter's temperature	-0.193	0.203	-0.952	0.339	0.704	21	0.041	-0.257	75.4
Mute Swan	8	Tree seed & berry crop	-0.179	0.150	-1.189	0.248	0.847	20	0.538	-0.027	62.6
Mute Swan	8	Previous winter's temperature	-0.245	0.150	-1.631	0.118	0.584	—	—	—	—
Mute Swan	8	Early winter temperature	0.661	0.149	4.428	<0.001	0.004	—	—	—	—
Whooper Swan	1	Intercept only (null model)	—	—	—	—	—	23	—	-0.206	74.1
Whooper Swan	2	Early winter temperature	<b>0.745</b>	<b>0.138</b>	<b>5.361</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>22</b>	<b>0.555</b>	<b>-0.199</b>	<b>58.2</b>
Whooper Swan	2	Previous winter's temperature	0.045	0.208	0.214	0.833	1.000	22	0.002	0.199	76.4
Whooper Swan	4	Tree seed & berry crop	0.032	0.208	0.152	0.881	1.000	22	0.001	0.210	76.4
Whooper Swan	4	Previous winter's temperature	-0.035	0.143	-0.246	0.808	1.000	21	0.557	-0.140	58.7
Whooper Swan	6	Tree seed & berry crop	0.084	0.141	0.593	0.560	1.000	21	0.562	0.180	58.4
Whooper Swan	6	Early winter temperature	0.751	0.141	5.313	<0.001	0.001	—	—	—	—
Whooper Swan	7	Tree seed & berry crop	0.026	0.215	0.123	0.903	1.000	21	0.003	0.203	69.0
Whooper Swan	7	Previous winter's temperature	-0.050	0.215	-0.232	0.815	1.000	21	0.003	0.203	69.0
Whooper Swan	8	Tree seed & berry crop	0.050	0.146	0.343	0.734	1.000	20	0.565	-0.151	71.1
Whooper Swan	8	Previous winter's temperature	-0.047	0.146	-0.324	0.749	1.000	—	—	—	—
Whooper Swan	8	Early winter temperature	0.757	0.145	5.206	<0.001	0.001	—	—	—	—
Mallard	1	Intercept only (null model)	—	—	—	—	—	23	—	-0.123	74.1
Mallard	2	Early winter temperature	0.026	0.208	0.128	0.901	1.000	22	0.001	0.221	75.8
Mallard	2	Previous winter's temperature	0.151	0.206	0.733	0.471	1.000	22	0.023	0.178	75.9
Mallard	4	Tree seed & berry crop	-0.297	0.199	-1.493	0.149	0.662	22	0.088	0.204	74.2
Mallard	4	Previous winter's temperature	0.150	0.212	0.708	0.487	1.000	21	0.023	0.177	76.5
Mallard	6	Tree seed & berry crop	-0.297	0.204	-1.456	0.160	0.698	21	0.088	0.204	76.8
Mallard	6	Early winter temperature	0.006	0.204	0.030	0.976	1.000	—	—	—	—
Mallard	6	Tree seed & berry crop	-0.321	0.201	-1.597	0.125	0.604	21	0.124	0.305	75.8
Mallard	7	Previous winter's temperature	0.191	0.201	0.951	0.352	1.000	22	0.041	0.157	76.1
Mallard	7	Tree seed & berry crop	-0.283	0.198	-1.429	0.151	0.685	20	0.125	0.306	76.5
Mallard	8	Previous winter's temperature	0.193	0.207	0.932	0.362	1.000	—	—	—	—
Mallard	8	Early winter temperature	-0.015	0.206	-0.075	0.941	1.000	—	—	—	—
Tufted duck	1	Intercept only (null model)	—	—	—	—	—	23	—	-0.231	74.1
Tufted duck	2	Early winter temperature	<b>0.571</b>	<b>0.171</b>	<b>3.32</b>	<b>0.003</b>	<b>0.033</b>	<b>22</b>	<b>0.436</b>	<b>-0.106</b>	<b>62.2</b>
Tufted duck	2	Previous winter's temperature	0.222	0.203	1.097	0.277	0.919	22	0.049	0.106	75.2
Tufted duck	4	Tree seed & berry crop	-0.147	0.206	-0.711	0.484	1.000	22	0.022	0.265	69.1
Tufted duck	4	Previous winter's temperature	0.171	0.172	0.996	0.330	1.000	21	0.355	0.094	68.1
Tufted duck	6	Early winter temperature	0.104	0.174	0.595	0.558	1.000	21	0.336	0.194	68.8
Tufted duck	6	Tree seed & berry crop	0.563	0.174	3.230	0.004	0.043	—	—	—	—
Tufted duck	7	Tree seed & berry crop	-0.177	0.206	-0.861	0.399	1.000	21	0.080	0.141	77.0
Tufted duck	7	Previous winter's temperature	0.244	0.206	1.185	0.249	0.847	—	—	—	—
Tufted duck	8	Tree seed & berry crop	0.185	0.176	1.052	0.293	0.847	20	0.371	0.138	70.5
Tufted duck	8	Previous winter's temperature	0.189	0.175	1.076	0.294	0.932	—	—	—	—
Tufted duck	8	Early winter temperature	0.544	0.174	3.115	0.005	0.056	—	—	—	—
Common Goldeneye	1	Intercept only (null model)	—	—	—	—	—	23	—	-0.291	74.1
Common Goldeneye	2	Early winter temperature	0.055	0.207	0.263	0.520	1.000	22	0.018	0.226	76.3
Common Goldeneye	2	Previous winter's temperature	0.109	0.207	0.525	0.604	1.000	22	0.012	0.290	76.2
Common Goldeneye	4	Tree seed & berry crop	-0.073	0.208	-0.351	0.729	1.000	21	0.005	0.292	76.3
Common Goldeneye	4	Previous winter's temperature	0.096	0.211	0.456	0.653	1.000	21	0.027	0.231	78.4
Common Goldeneye	6	Early winter temperature	0.125	0.211	0.593	0.559	1.000	—	—	—	—
Common Goldeneye	6	Tree seed & berry crop	-0.064	0.211	-0.301	0.758	1.000	21	0.022	0.289	78.5
Common Goldeneye	6	Early winter temperature	0.130	0.211	0.617	0.544	1.000	—	—	—	—
Common Goldeneye	7	Tree seed & berry crop	-0.088	0.213	-0.412	0.684	1.000	21	0.019	0.215	78.6
Common Goldeneye	7	Previous winter's temperature	0.120	0.213	0.563	0.579	1.000	—	—	—	—
Common Goldeneye	8	Tree seed & berry crop	-0.083	0.213	-0.389	0.698	1.000	20	0.033	0.226	81.1
Common Goldeneye	8	Previous winter's temperature	0.107	0.216	0.490	0.629	1.000	—	—	—	—
Common Goldeneye	8	Early winter temperature	0.119	0.216	0.548	0.589	1.000	—	—	—	—
Gosander	1	Intercept only (null model)	—	—	—	—	—	23	—	-0.217	74.1
Gosander	2	Early winter temperature	<b>0.705</b>	<b>0.148</b>	<b>4.762</b>	<b>&lt;0.001</b>	<b>0.002</b>	<b>22</b>	<b>0.496</b>	<b>-0.222</b>	<b>59.3</b>
Gosander	2	Previous winter's temperature	0.126	0.207	0.608	0.549	1.000	22	0.016	0.099	76.6
Gosander	4	Tree seed & berry crop	0.056	0.208	0.250	0.804	1.000	22	0.003	0.001	76.4
Gosander	4	Previous winter's temperature	0.052	0.152	0.367	0.717	1.000	21	0.500	-0.274	61.8
Gosander	6	Early winter temperature	0.189	0.152	1.241	<0.001	0.002	—	—	—	—
Gosander	6	Tree seed & berry crop	-0.051	0.152	-0.335	0.739	1.000	21	0.507	-0.233	61.4
Gosander	6	Early winter temperature	0.712	0.150	4.746	<0.001	0.002	—	—	—	—
Gosander	7	Tree seed & berry crop	0.037	0.213	0.174	0.863	1.000	21	0.017	-0.095	78.6
Gosander	7	Previous winter's temperature	0.121	0.213	0.569	0.575	1.000	—	—	—	—
Gosander	8	Tree seed & berry crop	-0.051	0.155	-0.335	0.739	1.000	20	0.509	-0.287	64.1
Gosander	8	Previous winter's temperature	0.043	0.155	0.274	0.786	1.000	—	—	—	—
Gosander	8	Early winter temperature	0.707	0.154	4.586	<0.001	0.003	—	—	—	—
New Gull	1	Intercept only (null model)	—	—	—	—	—	23	—	-0.017	74.1
New Gull	2	Early winter temperature	<b>0.507</b>	<b>0.160</b>	<b>3.22</b>	<b>0.003</b>	<b>0.03</b>				



Table S3. All models of trends in PoR. Model 1 is the null model (intercept only), model 2 is the model of linear change, and model 3 is the model of quadratic change (2<sup>nd</sup> order polynomial). Due to scaling (see text) the intercepts were always 0 and are not shown. Both unadjusted (p) and false discovery rate adjusted (FDR-p) p-values are shown. AICc is Akaike's information criterion for small sample size. The best models (the simplest models inside ΔAIC of 2) are bolded and the models used for detrending variables for the annual analyses (the most complex models inside ΔAIC of 2) are in italic.

Species	Model	Predictor	B	SE	t	p	FDR-p	df	r2	AICc
Waterbirds	Null	Intecept only	–	–	–	–	–	216	–	329.343
Waterbirds	Linear	Year	0.027	0.004	7.041	<0.001	–	215	–	295.820
<b>Waterbirds</b>	<b>Quadratic</b>	<b>Year</b>	<b>2.909</b>	<b>0.412</b>	<b>7.062</b>	<b>&lt;0.001</b>	–	<b>214</b>	–	<b>286.128</b>
<b>Waterbirds</b>	<b>Quadratic</b>	<b>Year<sup>2</sup></b>	<b>-0.620</b>	<b>0.412</b>	<b>-1.505</b>	<b>0.134</b>	–	–	–	–
<b>Terrestrial birds</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>432</b>	–	642.352
Terrestrial birds	Linear	Year	-0.0009	0.003	-0.294	0.769	–	431	–	654.032
Terrestrial birds	Quadratic	Year	-0.136	0.463	-0.293	0.769	–	430	–	645.551
Terrestrial birds	Quadratic	Year <sup>2</sup>	-0.164	0.463	-0.354	0.724	–	–	–	–
<b>Terrestrial non-frugivores</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>264</b>	–	<b>55.547</b>
Terrestrial non-frugivores	Linear	Year	-0.001	0.002	-0.508	0.612	–	263	–	67.823
Terrestrial non-frugivores	Quadratic	Year	-0.125	0.247	-0.507	0.612	–	262	–	61.119
Terrestrial non-frugivores	Quadratic	Year <sup>2</sup>	-0.078	0.247	-0.315	0.753	–	–	–	–
Mute Swan	Null	Intecept only	–	–	–	–	–	23	–	-1.244
<b>Mute Swan</b>	<b>Linear</b>	<b>Year</b>	<b>-0.013</b>	<b>0.006</b>	<b>-2.350</b>	<b>0.028</b>	<b>0.135</b>	<b>22</b>	<b>0.194</b>	<b>-4.251</b>
<i>Mute Swan</i>	<i>Quadratic</i>	<i>Year</i>	<i>-0.478</i>	<i>0.202</i>	<i>-2.359</i>	<i>0.028</i>	<i>0.135</i>	21	<i>0.235</i>	-2.975
<i>Mute Swan</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>-0.221</i>	<i>0.202</i>	<i>-1.093</i>	<i>0.286</i>	<i>0.537</i>	–	–	–
<b>Whooper Swan</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>18.268</b>
Whooper Swan	Linear	Year	-0.012	0.009	-1.344	0.192	0.432	22	0.073	18.749
<i>Whooper Swan</i>	<i>Quadratic</i>	<i>Year</i>	<i>-0.433</i>	<i>0.316</i>	<i>-1.370</i>	<i>0.185</i>	<i>0.426</i>	21	<i>0.146</i>	<i>19.287</i>
<i>Whooper Swan</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>0.434</i>	<i>0.316</i>	<i>1.374</i>	<i>0.183</i>	<i>0.426</i>	–	–	–
Mallard	Null	Intecept only	–	–	–	–	–	23	–	-47.586
<b>Mallard</b>	<b>Linear</b>	<b>Year</b>	<b>0.008</b>	<b>0.002</b>	<b>4.289</b>	<b>&lt;0.001</b>	<b>0.003</b>	<b>22</b>	<b>0.444</b>	<b>-59.907</b>
<i>Mallard</i>	<i>Quadratic</i>	<i>Year</i>	<i>0.286</i>	<i>0.067</i>	<i>4.299</i>	<i>&lt;0.001</i>	<i>0.003</i>	21	<i>0.471</i>	<i>-58.536</i>
<i>Mallard</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>0.070</i>	<i>0.067</i>	<i>1.052</i>	<i>0.304</i>	<i>0.559</i>	–	–	–
Tufted duck	Null	Intecept only	–	–	–	–	–	23	–	71.167
<b>Tufted duck</b>	<b>Linear</b>	<b>Year</b>	<b>0.105</b>	<b>0.015</b>	<b>6.920</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>22</b>	<b>0.676</b>	<b>45.398</b>
Tufted duck	Quadratic	Year	3.797	0.557	6.817	<0.001	<0.001	21	0.680	47.632
Tufted duck	Quadratic	Year <sup>2</sup>	0.316	0.557	0.568	0.576	0.810	–	–	–
Common Goldeneye	Null	Intecept only	–	–	–	–	–	23	–	43.569
<b>Common Goldeneye</b>	<b>Linear</b>	<b>Year</b>	<b>0.071</b>	<b>0.004</b>	<b>16.282</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>22</b>	<b>0.920</b>	<b>-17.256</b>
<i>Common Goldeneye</i>	<i>Quadratic</i>	<i>Year</i>	<i>2.552</i>	<i>0.158</i>	<i>16.153</i>	<i>&lt;0.001</i>	<i>&lt;0.001</i>	21	<i>0.922</i>	<i>-15.371</i>
<i>Common Goldeneye</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>-0.126</i>	<i>0.158</i>	<i>-0.798</i>	<i>0.434</i>	<i>0.709</i>	–	–	–
Goosander	Null	Intecept only	–	–	–	–	–	23	–	7.547
<b>Goosander</b>	<b>Linear</b>	<b>Year</b>	<b>0.028</b>	<b>0.005</b>	<b>5.850</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>22</b>	<b>0.598</b>	<b>-12.865</b>
Goosander	Quadratic	Year	1.001	0.175	5.721	<0.001	<0.001	21	0.598	-10.269
Goosander	Quadratic	Year <sup>2</sup>	0.005	0.175	0.027	0.978	0.999	–	–	–
<b>Mew Gull</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>30.686</b>
Mew Gull	Linear	Year	0.007	0.012	0.553	0.586	0.810	22	0.013	32.727
<i>Mew Gull</i>	<i>Quadratic</i>	<i>Year</i>	<i>0.235</i>	<i>0.390</i>	<i>0.604</i>	<i>0.552</i>	<i>0.810</i>	21	<i>0.210</i>	<i>29.754</i>
<i>Mew Gull</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>-0.913</i>	<i>0.390</i>	<i>-2.343</i>	<i>0.029</i>	<i>0.135</i>	–	–	–
<b>Herring Gull</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>30.771</b>
Herring Gull	Linear	Year	0.020	0.011	1.804	0.084	0.281	22	0.124	29.835
<i>Herring Gull</i>	<i>Quadratic</i>	<i>Year</i>	<i>0.725</i>	<i>0.387</i>	<i>1.873</i>	<i>0.074</i>	<i>0.268</i>	21	<i>0.223</i>	<i>29.434</i>
<i>Herring Gull</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>-0.648</i>	<i>0.387</i>	<i>-1.674</i>	<i>0.108</i>	<i>0.326</i>	–	–	–
Great Black-backed Gull	Null	Intecept only	–	–	–	–	–	23	–	19.079
Great Black-backed Gull	Linear	Year	0.029	0.007	3.978	0.001	0.005	22	0.408	8.362
<b>Great Black-backed Gull</b>	<b>Quadratic</b>	<b>Year</b>	<b>1.041</b>	<b>0.210</b>	<b>4.957</b>	<b>&lt;0.001</b>	<b>0.001</b>	<b>21</b>	<b>0.635</b>	<b>-1.151</b>
<b>Great Black-backed Gull</b>	<b>Quadratic</b>	<b>Year<sup>2</sup></b>	<b>-0.777</b>	<b>0.210</b>	<b>-3.703</b>	<b>0.001</b>	<b>0.010</b>	–	–	–
<b>Common Blackbird</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>11.000</b>
<i>Common Blackbird</i>	<i>Linear</i>	<i>Year</i>	<i>0.010</i>	<i>0.008</i>	<i>1.253</i>	<i>0.223</i>	<i>0.442</i>	22	<i>0.064</i>	<i>11.720</i>
Common Blackbird	Quadratic	Year	0.351	0.286	1.227	0.233	0.446	21	0.066	14.250
Common Blackbird	Quadratic	Year <sup>2</sup>	-0.070	0.286	-0.244	0.810	0.985	–	–	–
<b>Fieldfare</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>81.753</b>
Fieldfare	Linear	Year	-0.003	0.033	-0.086	0.932	0.999	22	0.000	84.117
Fieldfare	Quadratic	Year	-0.102	1.208	-0.085	0.933	0.999	21	0.015	86.353
Fieldfare	Quadratic	Year <sup>2</sup>	-0.684	1.208	-0.566	0.577	0.810	–	–	–
<b>Goldcrest</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>-24.011</b>
<i>Goldcrest</i>	<i>Linear</i>	<i>Year</i>	<i>-0.005</i>	<i>0.004</i>	<i>-1.287</i>	<i>0.211</i>	<i>0.442</i>	22	<i>0.067</i>	<i>-23.377</i>
Goldcrest	Quadratic	Year	-0.178	0.142	-1.259	0.221	0.442	21	0.068	-20.813
Goldcrest	Quadratic	Year <sup>2</sup>	-0.024	0.142	-0.170	0.866	0.987	–	–	–
<b>Blue Tit</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>-57.751</b>
<i>Blue Tit</i>	<i>Linear</i>	<i>Year</i>	<i>0.003</i>	<i>0.002</i>	<i>1.636</i>	<i>0.115</i>	<i>0.326</i>	22	<i>0.104</i>	<i>-58.131</i>
Blue Tit	Quadratic	Year	0.113	0.070	1.609	0.122	0.327	21	0.114	-55.808
Blue Tit	Quadratic	Year <sup>2</sup>	0.035	0.070	0.493	0.627	0.810	–	–	–
<b>Great Tit</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>-60.373</b>
Great Tit	Linear	Year	-0.004	0.002	-2.024	0.055	0.224	22	0.151	-62.101
<i>Great Tit</i>	<i>Quadratic</i>	<i>Year</i>	<i>-0.129</i>	<i>0.065</i>	<i>-2.001</i>	<i>0.058</i>	<i>0.227</i>	21	<i>0.169</i>	<i>-60.022</i>
<i>Great Tit</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>-0.044</i>	<i>0.065</i>	<i>-0.679</i>	<i>0.504</i>	<i>0.783</i>	–	–	–
<b>Eurasian Treecreeper</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>-40.656</b>
<i>Eurasian Treecreeper</i>	<i>Linear</i>	<i>Year</i>	<i>-0.003</i>	<i>0.003</i>	<i>-1.268</i>	<i>0.218</i>	<i>0.442</i>	22	<i>0.065</i>	<i>-39.972</i>
Eurasian Treecreeper	Quadratic	Year	-0.126	0.101	-1.246	0.226	0.442	21	0.075	-37.631
Eurasian Treecreeper	Quadratic	Year <sup>2</sup>	-0.048	0.101	-0.476	0.639	0.810	–	–	–
<b>Jackdaw</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>-24.111</b>
Jackdaw	Linear	Year	-0.0002	0.004	-0.041	0.967	0.999	22	0.000	-21.742
<i>Jackdaw</i>	<i>Quadratic</i>	<i>Year</i>	<i>-0.006</i>	<i>0.129</i>	<i>-0.046</i>	<i>0.964</i>	<i>0.999</i>	21	<i>0.229</i>	<i>-25.659</i>
<i>Jackdaw</i>	<i>Quadratic</i>	<i>Year<sup>2</sup></i>	<i>0.329</i>	<i>0.129</i>	<i>2.559</i>	<i>0.018</i>	<i>0.101</i>	–	–	–
<b>Hooded Crow</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>-87.346</b>
<i>Hooded Crow</i>	<i>Linear</i>	<i>Year</i>	<i>0.002</i>	<i>0.001</i>	<i>1.599</i>	<i>0.124</i>	<i>0.327</i>	22	<i>0.100</i>	<i>-87.609</i>
Hooded Crow	Quadratic	Year	0.061	0.039	1.567	0.131	0.338	21	0.104	-85.126
Hooded Crow	Quadratic	Year <sup>2</sup>	-0.012	0.039	-0.318	0.753	0.941	–	–	–
<b>Common Starling</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>44.987</b>
<i>Common Starling</i>	<i>Linear</i>	<i>Year</i>	<i>-0.014</i>	<i>0.016</i>	<i>-0.880</i>	<i>0.388</i>	<i>0.658</i>	22	<i>0.033</i>	<i>46.531</i>
Common Starling	Quadratic	Year	-0.494	0.567	-0.871	0.393	0.658	21	0.055	48.547
Common Starling	Quadratic	Year <sup>2</sup>	-0.408	0.567	-0.719	0.480	0.771	–	–	–
<b>Chaffinch</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>7.777</b>
Chaffinch	Linear	Year	0.001	0.008	0.067	0.947	0.999	22	0.000	10.143
Chaffinch	Quadratic	Year	0.018	0.277	0.066	0.948	0.999	21	0.004	12.646
Chaffinch	Quadratic	Year <sup>2</sup>	0.080	0.277	0.289	0.775	0.956	–	–	–
<b>Brambling</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>33.739</b>
Brambling	Linear	Year	-0.00001	0.013	-0.001	0.999	0.999	22	0.000	36.110
Brambling	Quadratic	Year	-0.0004	0.465	-0.001	0.999	0.999	21	0.002	38.656
Brambling	Quadratic	Year <sup>2</sup>	-0.100	0.465	-0.215	0.832	0.987	–	–	–
Greenfinch	Null	Intecept only	–	–	–	–	–	23	–	-32.979
<b>Greenfinch</b>	<b>Linear</b>	<b>Year</b>	<b>-0.009</b>	<b>0.003</b>	<b>-3.417</b>	<b>0.002</b>	<b>0.018</b>	<b>22</b>	<b>0.337</b>	<b>-40.871</b>
Greenfinch	Quadratic	Year	-0.334	0.099	-3.373	0.003	0.019	21	0.349	-38.736
Greenfinch	Quadratic	Year <sup>2</sup>	0.063	0.099	0.641	0.528	0.806	–	–	–
<b>Eurasian Siskin</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>56.457</b>
<i>Eurasian Siskin</i>	<i>Linear</i>	<i>Year</i>	<i>0.018</i>	<i>0.020</i>	<i>0.918</i>	<i>0.368</i>	<i>0.658</i>	22	<i>0.035</i>	<i>57.929</i>
Eurasian Siskin	Quadratic	Year	0.647	0.717	0.903	0.376	0.658	21	0.046	60.262
Eurasian Siskin	Quadratic	Year <sup>2</sup>	-0.347	0.717	-0.484	0.633	0.810	–	–	–
<b>Common Redpoll</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>37.760</b>
Common Redpoll	Linear	Year	-0.001	0.014	-0.056	0.955	0.999	22	0.000	40.128
Common Redpoll	Quadratic	Year	-0.028	0.505	-0.055	0.956	0.999	21	0.002	42.686
Common Redpoll	Quadratic	Year <sup>2</sup>	0.094	0.505	0.186	0.854	0.987	–	–	–
<b>Common Crossbill</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>	–	<b>62.936</b>
Common Crossbill	Linear	Year	-0.004	0.023	-0.178	0.860	0.987	22	0.001	65.273
Common Crossbill	Quadratic	Year	-0.145	0.826	-0.176	0.862	0.987	21	0.023	67.331
Common Crossbill	Quadratic	Year <sup>2</sup>	0.572	0.826	0.693	0.496	0.783	–	–	–
<b>Eurasian Bullfinch</b>	<b>Null</b>	<b>Intecept only</b>	–	–	–	–	–	<b>23</b>		

Table S4. All models of trends in tree crops (spruce and birch seeds, rowanberries) and winter temperatures. Every species has different temperatures because they were calculated species-specifically (see text for details). Model 1 is the null model, model 2 is the model of linear change, and model 3 is the model of quadratic change (2nd order polynomial). Due to scaling (see text) the intercepts were always 0 and are not shown. AICc is Akaike's information criterion for small sample size. The best models (the simplest models inside delta-AIC of 2) are bolded and the models used for detrending variables for the annual analyses (the most complex models inside delta-AIC of 2) are in italic.

Type	Species	Model	Predictor	B	SE	t	p	df	r2	AICc
<b>Seed and berry crop</b>	<b>Spruce</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>52.6</b>
<i>Seed and berry crop</i>	<i>Spruce</i>	<i>Linear</i>	<i>Year</i>	-0.014	0.018	-0.772	0.448	22	0.025	54.3
Seed and berry crop	Spruce	Quadratic	Year	-0.506	0.670	-0.755	0.458	21	0.027	56.9
Seed and berry crop	Spruce	Quadratic	Year <sup>2</sup>	-0.114	0.670	-0.170	0.867	21	0.027	56.9
<b>Seed and berry crop</b>	<b>Birch</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>14.1</b>
Seed and berry crop	Birch	Linear	Year	-0.002	0.009	-0.179	0.859	22	0.001	16.5
Seed and berry crop	Birch	Quadratic	Year	-0.055	0.314	-0.176	0.862	21	0.002	19.0
Seed and berry crop	Birch	Quadratic	Year <sup>2</sup>	0.048	0.314	0.153	0.879	21	0.002	19.0
<b>Seed and berry crop</b>	<b>Rowan</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>92.2</b>
Seed and berry crop	Rowan	Linear	Year	-0.003	0.041	-0.070	0.945	22	0.000	94.6
Seed and berry crop	Rowan	Quadratic	Year	-0.103	1.493	-0.069	0.946	21	0.011	96.9
Seed and berry crop	Rowan	Quadratic	Year <sup>2</sup>	0.738	1.493	0.494	0.626	21	0.011	96.9
<b>Early winter temperature</b>	<b>Mute Swan</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>113.6</b>
<i>Early winter temperature</i>	<i>Mute Swan</i>	<i>Linear</i>	<i>Year</i>	0.057	0.061	0.925	0.365	22	0.036	115.1
Early winter temperature	Mute Swan	Quadratic	Year	2.045	2.236	0.915	0.370	21	0.058	117.1
Early winter temperature	Mute Swan	Quadratic	Year <sup>2</sup>	-1.596	2.236	-0.714	0.483	21	0.058	117.1
<b>Early winter temperature</b>	<b>Whooper Swan</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>119.2</b>
<i>Early winter temperature</i>	<i>Whooper Swan</i>	<i>Linear</i>	<i>Year</i>	0.075	0.068	1.108	0.279	22	0.051	120.3
Early winter temperature	Whooper Swan	Quadratic	Year	2.718	2.479	1.097	0.285	21	0.073	122.3
Early winter temperature	Whooper Swan	Quadratic	Year <sup>2</sup>	-1.808	2.479	-0.730	0.473	21	0.073	122.3
<b>Early winter temperature</b>	<b>Mallard</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>119.2</b>
<i>Early winter temperature</i>	<i>Mallard</i>	<i>Linear</i>	<i>Year</i>	0.075	0.068	1.111	0.278	22	0.051	120.2
Early winter temperature	Mallard	Quadratic	Year	2.722	2.476	1.099	0.284	21	0.073	122.2
Early winter temperature	Mallard	Quadratic	Year <sup>2</sup>	-1.800	2.476	-0.727	0.475	21	0.073	122.2
<b>Early winter temperature</b>	<b>Tufted duck</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>116.6</b>
<i>Early winter temperature</i>	<i>Tufted duck</i>	<i>Linear</i>	<i>Year</i>	0.069	0.065	1.067	0.297	22	0.047	117.8
Early winter temperature	Tufted duck	Quadratic	Year	2.490	2.359	1.056	0.303	21	0.068	119.8
Early winter temperature	Tufted duck	Quadratic	Year <sup>2</sup>	-1.670	2.359	-0.708	0.486	21	0.068	119.8
<b>Early winter temperature</b>	<b>Common Goldeneye</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>118.4</b>
<i>Early winter temperature</i>	<i>Common Goldeneye</i>	<i>Linear</i>	<i>Year</i>	0.075	0.067	1.113	0.277	22	0.051	119.5
Early winter temperature	Common Goldeneye	Quadratic	Year	2.689	2.442	1.101	0.283	21	0.072	121.5
Early winter temperature	Common Goldeneye	Quadratic	Year <sup>2</sup>	-1.731	2.442	-0.709	0.486	21	0.072	121.5
<b>Early winter temperature</b>	<b>Goosander</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>118.3</b>
<i>Early winter temperature</i>	<i>Goosander</i>	<i>Linear</i>	<i>Year</i>	0.074	0.067	1.100	0.283	22	0.050	119.4
Early winter temperature	Goosander	Quadratic	Year	2.652	2.437	1.088	0.288	21	0.071	121.4
Early winter temperature	Goosander	Quadratic	Year <sup>2</sup>	-1.738	2.437	-0.713	0.483	21	0.071	121.4
<b>Early winter temperature</b>	<b>Mew Gull</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>118.1</b>
<i>Early winter temperature</i>	<i>Mew Gull</i>	<i>Linear</i>	<i>Year</i>	0.071	0.067	1.072	0.295	22	0.048	119.3
Early winter temperature	Mew Gull	Quadratic	Year	2.578	2.430	1.061	0.300	21	0.069	121.3
Early winter temperature	Mew Gull	Quadratic	Year <sup>2</sup>	-1.739	2.430	-0.716	0.482	21	0.069	121.3
<b>Early winter temperature</b>	<b>Herring Gull</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>118.3</b>
<i>Early winter temperature</i>	<i>Herring Gull</i>	<i>Linear</i>	<i>Year</i>	0.072	0.067	1.082	0.291	22	0.048	119.4
Early winter temperature	Herring Gull	Quadratic	Year	2.608	2.437	1.070	0.296	21	0.070	121.4
Early winter temperature	Herring Gull	Quadratic	Year <sup>2</sup>	-1.742	2.437	-0.715	0.482	21	0.070	121.4
<b>Early winter temperature</b>	<b>Great Black-backed Gull</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>114.0</b>
<i>Early winter temperature</i>	<i>Great Black-backed Gull</i>	<i>Linear</i>	<i>Year</i>	0.061	0.062	0.986	0.334	22	0.041	115.3
Early winter temperature	Great Black-backed Gull	Quadratic	Year	2.192	2.248	0.975	0.340	21	0.061	117.4
Early winter temperature	Great Black-backed Gull	Quadratic	Year <sup>2</sup>	-1.557	2.248	-0.692	0.496	21	0.061	117.4
<b>Early winter temperature</b>	<b>Common Blackbird</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>118.7</b>
<i>Early winter temperature</i>	<i>Common Blackbird</i>	<i>Linear</i>	<i>Year</i>	0.072	0.067	1.068	0.297	22	0.047	119.8
Early winter temperature	Common Blackbird	Quadratic	Year	2.597	2.458	1.057	0.302	21	0.069	121.9
Early winter temperature	Common Blackbird	Quadratic	Year <sup>2</sup>	-1.769	2.458	-0.720	0.479	21	0.069	121.9
<b>Early winter temperature</b>	<b>Fieldfare</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>119.9</b>
<i>Early winter temperature</i>	<i>Fieldfare</i>	<i>Linear</i>	<i>Year</i>	0.079	0.069	1.143	0.265	22	0.054	120.9
Early winter temperature	Fieldfare	Quadratic	Year	2.839	2.511	1.131	0.270	21	0.076	122.9
Early winter temperature	Fieldfare	Quadratic	Year <sup>2</sup>	-1.821	2.511	-0.725	0.476	21	0.076	122.9
<b>Early winter temperature</b>	<b>Goldcrest</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.2</b>
<i>Early winter temperature</i>	<i>Goldcrest</i>	<i>Linear</i>	<i>Year</i>	0.079	0.069	1.132	0.269	22	0.053	121.2
Early winter temperature	Goldcrest	Quadratic	Year	2.831	2.527	1.120	0.275	21	0.075	123.2
Early winter temperature	Goldcrest	Quadratic	Year <sup>2</sup>	-1.848	2.527	-0.732	0.472	21	0.075	123.2
<b>Early winter temperature</b>	<b>Blue Tit</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>119.9</b>
<i>Early winter temperature</i>	<i>Blue Tit</i>	<i>Linear</i>	<i>Year</i>	0.079	0.069	1.146	0.264	22	0.054	120.9
Early winter temperature	Blue Tit	Quadratic	Year	2.844	2.508	1.134	0.269	21	0.076	122.9
Early winter temperature	Blue Tit	Quadratic	Year <sup>2</sup>	-1.826	2.508	-0.728	0.474	21	0.076	122.9
<b>Early winter temperature</b>	<b>Great Tit</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.5</b>
<i>Early winter temperature</i>	<i>Great Tit</i>	<i>Linear</i>	<i>Year</i>	0.084	0.069	1.212	0.238	22	0.060	121.3
Early winter temperature	Great Tit	Quadratic	Year	3.036	2.531	1.200	0.243	21	0.082	123.3
Early winter temperature	Great Tit	Quadratic	Year <sup>2</sup>	-1.829	2.531	-0.723	0.478	21	0.082	123.3
<b>Early winter temperature</b>	<b>Eurasian Treecreeper</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.3</b>
<i>Early winter temperature</i>	<i>Eurasian Treecreeper</i>	<i>Linear</i>	<i>Year</i>	0.080	0.069	1.146	0.264	22	0.054	121.3
Early winter temperature	Eurasian Treecreeper	Quadratic	Year	2.868	2.529	1.134	0.269	21	0.076	123.3
Early winter temperature	Eurasian Treecreeper	Quadratic	Year <sup>2</sup>	-1.844	2.529	-0.729	0.474	21	0.076	123.3
<b>Early winter temperature</b>	<b>Jackdaw</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>118.8</b>
<i>Early winter temperature</i>	<i>Jackdaw</i>	<i>Linear</i>	<i>Year</i>	0.072	0.068	1.065	0.298	22	0.047	119.9
Early winter temperature	Jackdaw	Quadratic	Year	2.594	2.461	1.054	0.303	21	0.070	121.9
Early winter temperature	Jackdaw	Quadratic	Year <sup>2</sup>	-1.803	2.461	-0.732	0.472	21	0.070	121.9
<b>Early winter temperature</b>	<b>Hooded Crow</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.2</b>
<i>Early winter temperature</i>	<i>Hooded Crow</i>	<i>Linear</i>	<i>Year</i>	0.081	0.069	1.176	0.251	22	0.057	121.1
Early winter temperature	Hooded Crow	Quadratic	Year	2.935	2.521	1.164	0.257	21	0.079	123.1
Early winter temperature	Hooded Crow	Quadratic	Year <sup>2</sup>	-1.829	2.521	-0.726	0.476	21	0.079	123.1
<b>Early winter temperature</b>	<b>Common Starling</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>116.7</b>
<i>Early winter temperature</i>	<i>Common Starling</i>	<i>Linear</i>	<i>Year</i>	0.068	0.065	1.047	0.306	22	0.045	117.9
Early winter temperature	Common Starling	Quadratic	Year	2.450	2.365	1.036	0.312	21	0.068	119.9
Early winter temperature	Common Starling	Quadratic	Year <sup>2</sup>	-1.706	2.365	-0.721	0.478	21	0.068	119.9
<b>Early winter temperature</b>	<b>Chaffinch</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>117.8</b>
<i>Early winter temperature</i>	<i>Chaffinch</i>	<i>Linear</i>	<i>Year</i>	0.072	0.066	1.090	0.287	22	0.049	118.9
Early winter temperature	Chaffinch	Quadratic	Year	2.602	2.413	1.079	0.292	21	0.070	120.9
Early winter temperature	Chaffinch	Quadratic	Year <sup>2</sup>	-1.706	2.413	-0.707	0.487	21	0.070	120.9
<b>Early winter temperature</b>	<b>Brambling</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>116.7</b>
<i>Early winter temperature</i>	<i>Brambling</i>	<i>Linear</i>	<i>Year</i>	0.068	0.065	1.049	0.305	22	0.046	117.9
Early winter temperature	Brambling	Quadratic	Year	2.456	2.368	1.037	0.311	21	0.066	120.0
Early winter temperature	Brambling	Quadratic	Year <sup>2</sup>	-1.624	2.368	-0.686	0.500	21	0.066	120.0
<b>Early winter temperature</b>	<b>Greenfinch</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>119.8</b>
<i>Early winter temperature</i>	<i>Greenfinch</i>	<i>Linear</i>	<i>Year</i>	0.079	0.069	1.145	0.264	22	0.054	120.7
Early winter temperature	Greenfinch	Quadratic	Year	2.836	2.502	1.134	0.269	21	0.076	122.7
Early winter temperature	Greenfinch	Quadratic	Year <sup>2</sup>	-1.817	2.502	-0.726	0.475	21	0.076	122.7
<b>Early winter temperature</b>	<b>Eurasian Siskin</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>119.5</b>
<i>Early winter temperature</i>	<i>Eurasian Siskin</i>	<i>Linear</i>	<i>Year</i>	0.075	0.068	1.101	0.282	22	0.050	120.6
Early winter temperature	Eurasian Siskin	Quadratic	Year	2.718	2.495	1.089	0.288	21	0.073	122.6
Early winter temperature	Eurasian Siskin	Quadratic	Year <sup>2</sup>	-1.822	2.495	-0.730	0.473	21	0.073	122.6
<b>Early winter temperature</b>	<b>Common Redpoll</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.5</b>
<i>Early winter temperature</i>	<i>Common Redpoll</i>	<i>Linear</i>	<i>Year</i>	0.084	0.070	1.204	0.241	22	0.059	121.3
Early winter temperature	Common Redpoll	Quadratic	Year	3.018	2.533	1.192	0.246	21	0.081	123.4
Early winter temperature	Common Redpoll	Quadratic	Year <sup>2</sup>	-1.830	2.533	-0.723	0.478	21	0.081	123.4
<b>Early winter temperature</b>	<b>Common Crossbill</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.4</b>
<i>Early winter temperature</i>	<i>Common Crossbill</i>	<i>Linear</i>	<i>Year</i>	0.082	0.069	1.189	0.247	22	0.058	121.3
Early winter temperature	Common Crossbill	Quadratic	Year	2.974	2.529	1.176	0.252	21	0.079	123.3
Early winter temperature	Common Crossbill	Quadratic	Year <sup>2</sup>	-1.815	2.529	-0.718	0.481	21	0.079	123.3
<b>Early winter temperature</b>	<b>Eurasian Bullfinch</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.4</b>
<i>Early winter temperature</i>	<i>Eurasian Bullfinch</i>	<i>Linear</i>	<i>Year</i>	0.083	0.069	1.196	0.244	22	0.059	121.3
Early winter temperature	Eurasian Bullfinch	Quadratic	Year	2.996	2.531	1.184	0.249	21	0.080	123.3
Early winter temperature	Eurasian Bullfinch	Quadratic	Year <sup>2</sup>	-1.827	2.531	-0.722	0.478	21	0.080	123.3
<b>Early winter temperature</b>	<b>Yellowhammer</b>	<b>Null</b>	<b>Intercept only</b>	—	—	—	—	<b>23</b>	—	<b>120.4</b>
<i>Early winter temperature</i>	<i>Yellowhammer</i>	<i>Linear</i>	<i>Year</i>	0.080	0.070	1.153	0.261	22	0.055	121.3

Table S5. Linear trends in components of PoR, winter abundance and summer abundance, in 30 partially migratory bird species, and in waterbirds (W), all terrestrial birds (T) and terrestrial non-frugivorous birds (T nf) as groups. Due to scaling (see text) the intercepts were always 0 and are not shown. Both unadjusted (p) and false discovery rate adjusted (FDR-p) p-values are shown.

Species	Group	Winter			Summer		
		b ± SE	p	FDR-p	b ± SE	p	FDR-p
Waterbirds	W	0.040 ± 0.005	<0.001	—	0.007 ± 0.002	<0.001	—
Terrestrial birds (all)	T	0.003 ± 0.003	0.276	—	0.004 ± 0.001	<0.001	—
Terrestrial birds (non-fr)	T nf	0.005 ± 0.002	0.023	—	0.006 ± 0.001	<0.001	—
Mute Swan	W	0.039 ± 0.013	0.006	0.016	0.030 ± 0.005	<0.001	<0.001
Whooper Swan	W	0.037 ± 0.008	<0.001	0.001	0.049 ± 0.004	<0.001	<0.001
Mallard	W	0.012 ± 0.002	<0.001	<0.001	0.004 ± 0.001	0.002	0.004
Tufted duck	W	0.093 ± 0.016	<0.001	<0.001	-0.013 ± 0.002	<0.001	<0.001
Common Goldeneye	W	0.072 ± 0.004	<0.001	<0.001	0.001 ± 0.002	0.442	0.492
Goosander	W	0.020 ± 0.005	0.001	0.004	-0.008 ± 0.002	0.001	0.003
Mew Gull	W	0.027 ± 0.027	0.324	0.405	0.005 ± 0.001	<0.001	<0.001
Herring Gull	W	0.042 ± 0.025	0.110	0.165	-0.002 ± 0.001	0.042	0.060
Great Black-backed Gull	W	0.023 ± 0.008	0.007	0.017	-0.006 ± 0.001	<0.001	<0.001
Common Blackbird	T	0.031 ± 0.008	<0.001	0.001	0.021 ± 0.001	<0.001	<0.001
Fieldfare	T	0.005 ± 0.033	0.891	0.954	0.007 ± 0.002	0.002	0.004
Goldcrest	T nf	-0.011 ± 0.005	0.024	0.049	-0.006 ± 0.004	0.122	0.155
Blue Tit	T nf	0.030 ± 0.003	<0.001	<0.001	0.026 ± 0.003	<0.001	<0.001
Great Tit	T nf	0.007 ± 0.001	<0.001	<0.001	0.010 ± 0.001	<0.001	<0.001
Eurasian Treecreeper	T nf	0.003 ± 0.003	0.320	0.405	0.007 ± 0.003	0.038	0.057
Jackdaw	T nf	0.024 ± 0.003	<0.001	<0.001	0.024 ± 0.002	<0.001	<0.001
Hooded Crow	T nf	-0.003 ± 0.001	0.030	0.053	-0.005 ± 0.001	0.001	0.001
Common Starling	T	-0.022 ± 0.015	0.145	0.207	-0.009 ± 0.002	<0.001	0.001
Chaffinch	T	0.001 ± 0.007	0.928	0.960	0.0002 ± 0.0006	0.797	0.825
Brambling	T nf	-0.008 ± 0.013	0.564	0.650	-0.008 ± 0.002	0.002	0.004
Greenfinch	T nf	0.019 ± 0.003	<0.001	<0.001	0.028 ± 0.003	<0.001	<0.001
Eurasian Siskin	T	0.022 ± 0.019	0.267	0.364	0.004 ± 0.002	0.100	0.137
Common Redpoll	T	-0.004 ± 0.012	0.723	0.804	-0.004 ± 0.004	0.429	0.492
Common Crossbill	T	-0.016 ± 0.022	0.467	0.561	-0.012 ± 0.008	0.131	0.158
Eurasian Bullfinch	T	-0.012 ± 0.005	0.038	0.063	-0.001 ± 0.005	0.859	0.859
Yellowhammer	T nf	-0.005 ± 0.002	0.010	0.021	-0.002 ± 0.001	0.124	0.155
Reed Bunting	T nf	0.00007 ± 0.016	0.996	0.996	-0.008 ± 0.002	<0.001	<0.001